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Social organization in ungulates: revisiting Jarman's hypotheses

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Professor Wolf Blanckenhorn
University of Zurich
Editor-in-Chief
Journal of Evolutionary Biology

25 February 2021

Dear Professor Blanckenhorn,

Please find attached our revised manuscript, "*Social organization in ungulates: revisiting Jarman's hypotheses* " for consideration as Research Paper in *Journal of Evolutionary Biology*.

We thank you, the Associate Editor for the thorough evaluation. We carefully checked all comments and suggestions, and carried out the revisions to address these issues. Please find attached the revised manuscript and our point-by-point responses to the Editor. We would also like to take this opportunity to express our thanks to the Editor for the positive feedback and helpful comments for correction or modification.

In addition, we carefully checked the whole text and cleared up ambiguities. We also changed the Discussion to highlight the scientific significance of re-analysing another textbook example of comparative sociobiology by Song, Liker, Yang & Székely, American Naturalist, in revision*. Given the significance of Jarman's analyses and the novel insights our work have produced, we believe these results will interest a broad range of evolutionary biologists.

We very much hope the revised manuscript is accepted for publication in *Journal of Evolutionary Biology*.

Sincerely yours,

Karola Szemán
PhD student, on behalf of all authors

*Song, Z., Liker, A., Liu, Y. & Székely, T. Evolution of social organization: phylogenetic analyses of ecology and sexual selection in weavers. American Naturalist, in revision.

Social organization in ungulates: revisiting Jarman's hypotheses
Responses to reviewers' comments

Text by the Editor and Reviewers are in Times New Roman font, whereas our responses in **bold Arial Black font.** Line numbers refer to the revised MS.

EDITOR'S COMMENTS TO THE AUTHORS

Editor: Dr Julia Schroeder
Comments to the author:

Dear Author,

Thank you for submitting your manuscript "Social organization in ungulates: revisiting Jarman's hypotheses" (JEB ms JEB-2020-00430.R1) to the Journal of Evolutionary Biology. I have found a number of points that preclude it from being acceptable for publication in its present form. I also liked your paper, and I am therefore willing to consider it further for acceptance provided that you revise it appropriately along the lines recommended below.

We appreciate the positive evaluation.

Minor comments:

Abstract - ten families (instead of 10 families)

Thank you, corrected (Line 8).

Introduction -third to last paragraph, last sentence: "a well-cited study as indicated b1462 citations" Do you mean "by 1462"? And maybe update the numbers while you're at it

Thank you, corrected and updated (Lines 76-77).

Material and Methods - first sentence - "thammals" - is it "the mammals"?

Thank you, corrected (Line 104).

Statistical analysis, second paragraph:
"hypothesizes" - do you mean "hypotheses"?

Thank you, corrected (Line 139).

Can you clarify to me what you mean with "bivariate models" - you write you only have one response (body size), not two, as is usual in a bivariate model.

Bivariate models could be used in different contexts, although it seems we use it in the commonest sense (Wikipedia accessed 24 February 2021: *"Bivariate analysis …involves the analysis of two variables (often denoted as X, Y), for the purpose of determining the empirical relationship between them."* We clarified the models' structure in the text (Line 139).

As to your "third set" of PGL analyses, this requires some clarification in the text.
You say two included group size as explanatory variable - was that the only explanatory variable - please state that. The third model please also again confirm what is the response - I assume mating system? If so, how is this different from the previous model?

Thank you, we added explanation to this part (Lines 147-152).

Phylogenetic path analysis - you say you repeated this process for each variable - can you confirm in text which variables that are.

Thank you, we clarified the list of the used variables (Line 170).

Discussion
middle of third paragraph: "Giraffa camelopardalis) are taller thanfemales" - missing space

Thank you, corrected (Line 267).

Second to last paragraph, first sentence: "Our study, however, have several" -> has

Thank you, corrected (Line 332).

Social organization in ungulates: revisiting Jarman's hypotheses

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Data Accessibility Statement: Data and all scripts will be made publicly available

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Competing interests: The authors have declared that no competing interests exist.

Social organization in ungulates: revisiting Jarman's hypotheses

Abstract

Ungulates (antelopes, deer and relatives) have some of the most diverse social systems among mammals. To understand the evolution of ungulate social organisation, Jarman (1974) proposed an ecological scenario of how distribution of resources, habitat and feeding style may have influenced social organisation. Although Jarman's scenario makes intuitive sense and remain a textbook example of social evolution, it has not been scrutinised using modern phylogenetic comparative methods. Here we use 230 ungulate species from ten families to test Jarman's hypotheses using phylogenetic analyses. Consistently with Jarman's proposition, both habitat and feeding style predict group size, since grazing ungulates typically live in open habitats and form large herds. Group size, in turn, has a knock-on effect on mating systems and sexual size dimorphism, since ungulates that live in large herds exhibit polygamy and extensive sexual size dimorphism. Phylogenetic confirmatory path analyses suggest that evolutionary changes in habitat type, feeding style and body size directly (or indirectly) induce shifts in social organisation. Taken together, these phylogenetic comparative analyses confirm Jarman's conjectures, although they also uncover novel relationships between ecology and social organization. Further studies are needed to explore the relevance of Jarman (1974) scenario for mammals beyond ungulates.

Keywords: Artiodactyla, social evolution, mating system, group size, habitat, feeding style, phylogenetic path analysis, phylogenetic generalized least squares

Introduction

One of the core tenets in behavioral ecology and sociobiology is that spatial and temporal distribution of resources influence social organization (Crook, 1964; Wilson, 1975; Alcock, 2013; Davies et al., 2012). Thus, the availability of food resources, breeding sites along with predators and parasites are expected to influence territoriality, group formation and colonial breeding (Estes, 1974; Krause & Ruxton, 2002; Clutton-Brock, 2016). Specifically, group formation and group size are thought to be influenced by various costs and benefits of group living in a particular environment. Benefits of group formation, for instance enhanced feeding efficiency, defense against predators, access to potential mates, may be negated by the cost of group living such as increased competition for food and mates, increased detectability by predators, and a higher chance of infections by diseases and parasites (Krause & Ruxton, 2002; Davies et al., 2012; Clutton-Brock, 2016).

Artiodactyla (antelopes, deer, bovids and relatives, approx. 250 species; ungulates henceforth) is one of the most diverse mammalian order, since body size vary several magnitudes between species, they inhabit six continents and they live in diverse habitats that include deserts, grasslands and forests. In addition, their social behaviour, breeding system and associated traits such as sexual size dimorphism (SSD) are also highly variable (Jarman, 1974; Pérez-Barbería et al., 2002; Wilson & Mittermeier, 2011; Clutton- Brock, 2016). In a seminal study, Jarman (1974) conjectured that interspecific variation in ecology and social organization of ungulates are associated. Following Crook's (1964) pioneering work on social organization in weaverbirds (*Ploceidae*), Jarman (1974) laid the foundations of behavioral ecology and sociobiology by adopting an ecological cross-species thinking that has became known as the comparative approach (Felsenstein, 1985; Harvey & Pagel, 1991).

Jarman (1974) focused on African antelopes, and he recognized five groups based on their ecology, primarily habitat and feeding style. He noticed that body size, mating systems, sexual size dimorphism and anti-predator behaviour tend to match the ecological conditions. He argued that body size should be associated with metabolic rate since metabolic requirement per unit weight is higher in small-bodied species. Therefore, small-bodied ungulates are expected to select more nutritious and higher calorie content food items such as fresh leaves and berries. Since these items are often scarce and dispersed, small-bodied ungulates are expected to hold territories alone or in pairs to monopolize food-resources. In contrast, large-bodied species can feed on lower quality food in bulk such as grasses, and since this type of food is less defensible economically the large-bodied ungulates roam in herds. Jarman (1974) synthetized these relationships into an evolutionary scenario whereby polygamy and sexual size dimorphism was a consequence of habitats (i.e., closed forests versus open savannah) and feeding styles (i.e., browsers versus grazers) via metabolic demands of having a small or large body size (Fig. 1a). Jarman's arguments were based on the idea that habitat types and feeding styles may influence the spatial distribution of females, that in turn have knock-on effect on males' strategy to secure mating rights. Females' tendency to aggregate seasonally or all-year-round create an opportunity for males to monopolize mating rights and thus facilitate the evolution of polygamous matings. Given the high mating stakes in polygamous systems, male-male conflicts are expected to intensify leading to increased male body size, and ultimately, to extensive sexual size dimorphism and elaboration of different weaponries including horns and antlers (Geist, 1966; Jarman, 1974).

Jarman (1974) stimulated much follow up studies and it became one of the best-cited examples of the impact of resource distribution on social organization (Emlen & Oring, 1977; Greenwood, 1980; Wittenberger, 1981; Clutton-Brock, 1989; Shultz et al., 2011; Clutton-

Brock, 2016; Bravo et al., 2019; Jaeggi et al., 2020; Lukas & Clutton-Brock, 2020; Winternon et al., 2020). As a result, the ungulates became a prime example of comparative approach (Wittenberger, 1981; Harvey & Pagel, 1991; Davies et al., 2012; Clutton-Brock, 2016). Consistently, it is a well-cited study as indicated by 1484 citations in Web of Science and 2359 citations in Google Scholar (accessed on 24.02.2021).

However, Jarman's study has limitations (Davies et al., 2012). First, the core hypotheses are limited to African ungulates, and thus the validity of his arguments for ungulates as whole has remained uncovered. Second, Jarman did not use statistical analysis to test the putative associations between ecology and social organization. Third, phylogenetic history can create erroneous impressions about trait evolution and can create statistical artefacts, and therefore, we need to incorporate phylogenetic signals in statistical analyses. As yet, Jarman's hypotheses have not been evaluated by modern phylogenetic comparative analyses except Pérez-Barbería et al. (2002) that investigated the origin of sexual size dimorphism among ungulates using a binary character evolution analysis. Whilst Pérez-Barbeíra et al. (2002) uncovered important associations, they (i) have not included ecological variables in their analyses although the ecological variables were key components of Jarman's scenario, and (ii) assessed bivariate associations only, and therefore the overall fit of data to Jarman's scenario has remained untested.

Here we revisit Jarman's (1974) hypotheses using phylogenetically controlled analyses. Using data from 230 ungulate species worldwide from 10 families, recent phylogenetic hypotheses and modern phylogenetic methods, we investigate (1) whether habitat type and feeding style predict body size, (2) whether habitat and feeding style predict group size, and (3) the associations between group size, mating system and sexual size dimorphism. By using phylogenetic confirmatory path analyses (Santos and Cantanella, 2011; Santos, 2012; Gonzalez-Voyer & von Hardenberg, 2014), (4) we also test the fits of several evolutionary hypotheses – including Jarman's scenario – to the data.

Material and Methods

Data Collection

We collected ecological and behavioural data from textbooks including the Handbook of the Mammals of the World (part 2, Hoofed Mammals; Wilson and Mittermeier, 2011), peer-reviewed papers and books, published IUCN reports on ungulate ecology and life history (Supplementary material 1; distribution of the data among ungulate families are given in Supplementary material 2 Table S1). We targeted all ungulate species listed in the Handbook of the Mammals of the World (Wilson & Mittermeier, 2011) except: (1) species that were extinct and extinct in the wild according to their IUCN categories, and (2) domesticated species and subspecies. In total, we obtained data on 230 Artiodactyla species representing all ten extant families.

We used group size as one of the indicators of social organization defined as the mean number of individuals in a group. For species where there were no available data for mean number of individuals, we calculated it as the mean value of minimum and maximum group size. We used mating system as a further proxy of social organization, defined as a binary variable: we considered a species polygamous if the individuals typically have more than one mate per breeding season and monogamous if individuals of both sexes have only one mate per breeding season. Habitat types were classified as open or closed: open-habitat dwelling species were those that spend most of the year in habitats with low vegetation like grasses whereas closed-habitat dwelling species were those that live in dense habitats such as forests.

Feeding style was scored as a binary trait: grazer or not-grazer. Grazers were those species that predominantly feed on grasses, whereas non-grazers feed on the leaves and branches of trees and shrubs and may also consume fruits, mushrooms or even some animals. Male and female body size were expressed in kg, and we calculated average body size as the average of female and male mass. We calculated sexual size dimorphism (SSD) as $\log_{10}$ (male body size / female body size) following Fairbairn et al. (2007).

Statistical Analyses

Phylogenetic Generalized Least Squares Models

We analyzed the relationships between the variables using Phylogenetic Generalized Least Squares (PGLS, Freckleton et al., 2002), that controls for the phylogenetic non-independence among species. The analyses were conducted in the R software (version 3.5.3.; R Core Team, 2016), with package 'caper' (Orme & Freckleton, 2013). We used the phylogenetic tree published by Bininda-Emonds et al. (2007) to represent phylogenetic relationships between species, because this is the most complete phylogenetic tree for mammals.

To test specific hypotheses, we conducted eight bivariate (with one response variable and one explanatory variable in each model) PGLS models. We grouped the models into three sets, according to the structure of relationships proposed by Jarman (Fig. 1a). The first set of analyses investigated the putative factors related to body size. The bivariate models included habitat type and feeding style as explanatory variables (one predictor in each model) and body size as response variable. The second set of models focused on group size: here we had three bivariate models in which group size was the response variable and body size, feeding style and habitat type were the explanatory variables. The third set of PGLS analyses comprised of three bivariate models. The first model included group size as response variable and SSD as explanatory variable. In the second model group size was the response variable and mating system appeared as explanatory variable. The third model investigated the association between mating system and SSD where SSD was included as response variable and mating system as explanatory variable. Group size and body size were log-transformed prior to the analysis.

Phylogenetic Path Analysis

To investigate further the structure of relationships between ecological factors and components of social organization, we applied phylogenetically controlled path analyses, a method that was suggested for testing direct and indirect relationships among a set of variables (Gonzalez-Voyer & von Hardenberg, 2014).

To find the best fitting path model to the data, we followed the method proposed by Santos and Canatella (2011) and Santos (2012), using the R package ‘piecewieseSEM’ (Lefcheck, 2016). Before the path analysis we transformed the data phylogenetically, so we were able to control for phylogenetic relatedness among species (Santos, 2012). For the latter purpose, we (1) determined Pagel’s λ (a measure of the strength of phylogenetic signal in the data) separately for each variable by PGLS models using maximum likelihood, (2) used this variable-specific λ value to re-scale the phylogenetic tree to a unit tree, and (3) used the transformed tree to calculate phylogenetically independent contrasts for the variable by the 'pic' function of the 'ape' R package (Paradis, 2012). We repeated this process for each variable (body size, feeding style, habitat type, group size, mating system and SSD), and the resulting phylogenetically transformed values were used for fitting path models (see Santos (2012) for a similar approach).

Our approach for finding the best fitting model was based on a model selection procedure proposed by Santos and Canatella (2011) and Santos (2012). We used Jarman's (1974) hypothesis as a starting model (Fig. 1a). According to this model, we created a full initial (i.e. just-identified) model which included all the pathways between the variables (Supplementary material 2 Fig. S1). After fitting the full initial model, we excluded the non-significant pathways from the model one-by-one. In each step, we eliminated the path which had the path coefficient with the highest p value, then re-fitted the new, reduced model to the data. We had seven steps until a model with the acceptable fit was reached. Model fit was evaluated by Fisher C statistics. The C statistic tests the goodness of fit of the whole path model, and the model is rejected, i.e. it does not provide a good fit to the data, if the result of this C statistic is statistically significant (and conversely a statistically non-significant result means acceptable fit; Lefcheck 2016). In the accepted model all the pathways had path coefficient with less than 0.05 p value (Supplementary material 2 Table S2).

Results

Diversity in Ecology and Social Organisation of Ungulates

Ecology, body mass and social organisation are highly variable among ungulates (Supplementary material 2 Fig.S2, S3): 84 species live in forests whereas 112 species live in open habitats (we have no habitat data for 34 species, Supplementary material 2 Table S1). Body size varies between 1.3 kg (smallest) to 1,600 kg (largest), and body size dimorphism ranges between male-biased SSD (N = 133 species, males larger in average by 26%) to female-biased SSD (N = 34 species, females are larger in average by 10%) (we have no data on degree of SSD of 63 species, see in Supplementary material 2 Table S1). Importantly, the variation in ecology, body size and social organisation are scattered across the ungulate phylogeny (Fig. 2).

Ecology, Body Size and Group Size

Both feeding style and habitat correlate with body size, since grazers are larger than not-grazers (PGLS, $F_{159} = 6.059$, $p = 0.014$, N = 148 species; Table 1, Fig. 3a), and ungulates that live in open habitats are larger than those that live in closed habitats (PGLS, $F_{147} = 23.81$, $p < 0.01$, N = 148 species; Table 1, Fig. 3b). These differences are consistent with sex specific data (Supplementary material 2 Fig. S4).

Feeding style and habitat also associate with group size, since grazers live in larger groups than browsers (PGLS, $F_{175} = 26.14$, $p < 0.001$, N = 177 species; Table 1, Fig. 3c), and open-habitat dwelling species live in larger groups then those in closed habitats (PGLS, $F_{157} = 22.40$, $p < 0.001$, N = 159 species; Table 1, Fig. 3d). Consistently, body size and group size are associated since large-bodied species live in groups whereas small ones usually live alone or in pairs (PGLS, $F_{148} = 31.73$, $p < 0.01$, N = 148 species; Table 1, Fig. 4a).

Mating System and Sexual Size Dimorphism (SSD)

Consistently with Jarman's arguments, group size is associated with the extent of sexual size dimorphism, since species that live in larger groups exhibit more male-biased SSD (PGLS, $F_{148} = 23.90$, $p < 0.001$, N = 150 species; Table 1, Fig. 4b). Furthermore, polygamous ungulates live in larger groups than monogamous ones (PGLS, $F_{92} = 76.61$, $p < 0.001$, N = 94 species; Table 1, Fig. 5a). Consistently, SSD and mating system are also associated: in polygamous ungulates the males are usually larger than females, whereas monogamous ungulates typically exhibit monomorphism or female-biased SSD (PGLS, $F_{100} = 53.95$, $p < 0.001$, N = 102 species; Table 1, Fig. 5b). The diagnostic plots for the models are provided in Supplementary Material Fig. S5.

Phylogenetic Path Analyses

Phylogenetic confirmatory path analysis supported most components of Jarman's (1974) scenario, although it also uncovered several additional relationships (Fig. 1a, b). The best fitting path model has statistically acceptable fit to the data (Fisher's C = 15.7, $df = 12$, $p = 0.206$; Fig. 1b). Consistently with Jarman's arguments, body size is associated with habitat type, and both habitat type and feeding style are associated with group size in the best supported model (Fig 1b). Furthermore, the proposed associations were confirmed between mating system, group size and SSD (Fig. 1., Supplementary material 2 Table S2), although not the one between body size and feeding style (Fig. 1., Supplementary material 2 Table S2). Importantly, the best model uncovered novel relationships that were not conjectured by Jarman that include association between body size and group size, and those between habitat type, feeding style and mating system (Fig. 1., Supplementary material 2 Table S2).

Discussion

Our study has revealed three major patterns. First, increased body size appears to trigger the evolution of different social systems and mating strategies among ungulates (Geist, 1974; Bell, 1971; Perez-Barbería et al., 2002, Davies et al. 2012; Clutton-Brock, 2016). These results support Jarman's (1974) hypotheses and expose robust differences among different species. Body size is the main predictor of ecological variables, whereas ecological variables have significant effect on social organization. To satisfy their metabolic requirements, small-bodied species need lower amount of food but higher quality, compared to large-bodied species. Because of this trade-off between food quality and quantity, small-bodied ungulates have more time during the day to find appropriate food items compared to larger species (Bell, 1971; Jarman, 1974; Owen-Smith & Novellie, 1982). Since high-quality food items appear to occur in higher density in closed habitats (e.g. forest, shrublands), small-bodied ungulates tend to be closed-habitat dwelling species, whereas larger species forced to live in open fields where they can consume substantial amount of food (Kleiber, 1947; Bell, 1971; Jarman, 1974; Jarman & Sinclair, 1979).

Since open-habitat dwelling species seem more vulnerable to predators than species that live in closed habitats, group living and large body size are considered as adaptations to reduce predation risk via detecting and/or deterring predators (Capellini, 2006). Consistently with these expectations, our results confirm that large ungulates tend to live in groups, and group living ungulates typically inhabit open habitats (e.g. savannah).

Second, our study show that group size was associated with different mating strategies among Artiodactyls. Living in groups increases the probability of polygamy and may amplify sexual selection (Jarman, 1974; Pérez-Barbería et al., 2002; Gordon & Pagel, 2002). More intense sexual selection could be responsible for larger SSD in polygamous species than in monogamous ones (Pérez-Barbería & Grodon, 2000; Pérez-Barbería et al., 2002). Sexual size dimorphism may also be advantageous for dividing the resources between males and females that can reduce intersexual competition (Fairbairn et al. 2007). For example, male kudus (*Tragelaphus strepsiceros*) and giraffes (*Giraffa camelopardalis*) are taller than females and capable of feeding on tall bushes and trees (Ginnet & Demmet, 1997; Mysterud, 2000; du Toit, 2005; Main and du Toit, 2005). In red deer (*Cervus elaphus*) and some African antelopes males and females live separately during the year and exhibit different habitats, feeding strategies and time-budgets (Staines & Crisp, 1978; Clutton-Brock et al., 1982; Conrad et al., 2000; du Toit, 2005; Main & du Toit, 2005; Lindsay, 2011). The latter patterns occur in other mammals as well: in arboreal primates males are heavier and unable to climb as high as females in the canopy, thus their foraging behaviour differs from the females' foraging strategies (Clutton-Brock, 1977; Grassi, 2002). These ecological differences between sexes may imply different energy intake rates and energy requirement of males and females in sexually dimorphic species (Clutton-Brock et al., 1987; Pérez-Barbería & Gordon, 1998). This in turn would suggest that some males in strongly dimorphic species may be forced into secondary habitats due the strong intersexual competition for females and this may increase mortality among males (Bowyer 2004; du Toit 2015, Clutton-Brock 2016). Due to the variety of ecological and sexual selective processes between males and females that have implications for body sizes, the jury is still out there how these different processes shape body sizes of males, females and/or of both sexes (reviewed by De Lisle 2019).

Third, using phylogenetic path analysis we confirmed several elements of Jarman's scenario, and also highlighted additional associations. As proposed by Jarman (1974), our best model supports that body size is related to habitat type, whereas a species' ecology predict group size, group size presages the type of mating system and mating system predicts the degree of SSD. It appears that the available forest habitats have decreased in the Miocene (Janis, 1982), and forest fragmentation may have forced ancestral ungulates into open habitats. Increased group size possibly evolved to reduce predation risk in the new habitat. With large social groups possibly came the opportunity for males to monopolize mating opportunities and this favored the evolution of polygamy. With polygamy male-male conflicts also escalated, which possibly led to extensive sexual dimorphism and the appearance of weaponry (Geist, 1974; Pérez-Barbería et al., 2002).

Our path analysis – consistently with a recent re-analysis of Crook (1964) hypotheses of weavers social organization (Song et al. unpublished data) – suggest that field based intuition can identify evolutionary scenarios that are supported by modern phylogenetic analyses. However, both our work on ungulates and Song et al. (unpublished data) on weavers suggest novel relationships not envisaged by Jarman and Crook, respectively. For example, phylogenetic confirmatory path analysis has uncovered a direct effect of body size on group size in ungulates. A possible explanation is that parallel with increased body size predation risk also increased which may have favoured the evolution of different anti-predator strategies, like group living (Krause & Ruxton, 2002). The direct effect of species' ecology on mating system was also a new relationship uncovered by the phylogenetic path analysis. Jarman seems to have considered only the social route to polygamy, although polygamy may have a direct ecological route as well: structure of the habitat and feeding style, due resource distribution, should promote the opportunity to defend key resources and/or mates. Without favourable ecological conditions, maintaining polygamy can be too costly, therefore animals may adopt alternative strategies (Emlen & Oring, 1977).

The best path model does not support one element of Jarman's hypothesis: the effect of body size on feeding style. This can be a consequence of that other variables – not included in our study – influenced feeding style (e.g. anatomical changes), and/or methodological limitations, for example the high ratio of binary variables and multi-collinearity between some predictors can affect the results of phylogenetic path analysis. Future comparative analyses with refined data could shed light on these alternatives.

Recent studies, however, suggest additional ecological and social factors in the evolution of mating systems that have not been envisaged in Jarman's time. First, population density seems to have a major impact on mating system variation in mammals (Lukas & Clutton-Brock, 2013). Specifically, when densities are low, males cannot monopolise several females, so that monogamy more likely occur than polygamy (Lukas & Clutton-Brock, 2013). Second, harsh and/or extreme climate has been shown to facilitate cooperation between group members and also, may induce male and female permanent association and males' involvement in care (West & Capellini, 2016; Shen et al., 2017). Such effects of extreme climatic events have been shown in birds and in rodents, although their influence may be more general (Rubenstein & Lovette, 2007; Firman et al., 2020). Third, recent studies suggest that the social environment – as characterised by adult sex ratio (ASR) – can facilitate certain mating systems and parenting in humans and birds since when one sex is more abundant in the population than the other, this would increase the mating opportunities of the rarer sex, and thus facilitate polygamy by the rarer sex (Liker et al., 2013; Székely et al. 2014; Schacht et al., 2015, 2017). Phylogenetic comparative analyses will be useful to explore these processes that go beyond Jarman's conjectures.

Our study, however, has five main limitations. First, here we focus on Jarman's scenario, and we did not explicitly investigate additional variables that may influence social organization, for example timing of breeding and/or spatial and temporal variation in resources (Clutton-Brock, 1989; Davies et al., 2012; Clutton-Brock 2016). Further analyses are needed to address these aspects of ungulate social organization. Second, we assume a single data point for each variable for a given species. This may not be the case, since body size, group size and mating systems may all be variable within a species. This variation could be due to age differences, or to geographic variation that produces differences between distant populations. Jaeggi et al. (2020) recently argued that majority of ancestral and extant ungulates exhibit variation in their social behavior and comparative studies should consider intraspecific variations in the analyses of social organization. Whilst we fully agree with the spirit of Jaeggi et al. (2020), we note that lack of data from different breeding populations could limit the power of such analyses especially if the objective is to explore broad-scale patterns for hundreds of species. Third, we used a single phylogenetic hypothesis, and this can be erroneous. With increasing availability of genomic data, this limitation can be overcome by using hundreds of phylogenetic hypotheses simultaneously. Fourth, here we used bivariate PGLS models to obviate interdependence between explanatory variables and therefore some association between variables may stayed uncovered. To resolve interdependence among ecological, social and life-history data, we need further analysis with higher resolution data. Finally, phylogenetic comparative analyses are designed to investigate associations but not causation. Even in phylogenetic path analyses, the directionality of associations are confirmatory rather than causative such as in an experimental work.

In conclusion, our study supports Jarman's scenario by suggesting that body size is an important trait in social evolution of ungulates. To satisfy their metabolic needs, different species live in several different habitats across the globe hence it demands different strategies in different species to thrive. Thus, wide range of social organization evolved in ungulates, together with various reproductive strategies. To further advance studies of social organization, it will be important to quantify the ecology, behaviour and natural history of yet unstudied species. A more detailed understanding on ungulates social organization will provide important contribution to understanding of evolution of Artiodactyla and move forward evolutionary understanding and the conservation of threatened species and their habitats.

References

Alcock, J. (2013). Animal Behavior (10th ed.). Oxford University Press, Oxford.

Bell, R.H.V. (1971). A grazing ecosystem in the Serengeti. Scientific American, 255, 86-93.

Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M., Grenyer, R. D., Price, S. A., Vos, R. A., Gittleman, J. L. & Purvis, A. (2007). The delayed rise of present-day mammals. Nature, 446, 507- 512. https://doi.org/10.1038/nature05634

Bowyer, R.T. (2004). Sexual segregation in ruminants: definitions, hypotheses and implication for conservation and management. Journal of Mammology, 85: 1039-1052. https://doi.org/10.1644/BBL-002.1

Bravo, C., Bautista, L.M., Ponce, C. & Alonso, J.C. (2019). Feeding functional responses in sexually size-dimorphic bird. Acta Oecologica, 101, 103487. https://doi.org/10.1016/j.actao.2019.103487

Capellini, I. (2006). Evolution of body size in the genus *Damaliscus*: a comparison with hartebeest *Alcelahus* ssp. Journal of Zoology, 270, 139-146. https://doi.org/10.1111/j.1469-7998.2006.00100.x

Clutton-Brock, T.H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In T.H. Clutton- Brock (Ed.), Primate ecology: studies of feeding and ranging behaviours in Lemurs, Monkeys and Apes (pp. 539-556). London, UK: Academic Press.

Clutton-Brock, T.H. (1982). Sexual selection in the Cervidae. In C.M. Wemmer (Ed.), Biology and Management of the Cervidae (pp. 110–122). Washington, US: Smithsonian Institution Press.

Clutton-Brock, T.H. (1989). Mammalian mating systems. Proceeding of the Royal Society London B, 236, 339-372. https://doi.org/10.1098/rspb.1989.0027

Clutton-Brock, T.H. (2016). Mammal Societies. Chichester, UK: John Wiley and Sons Inc.

Clutton-Brock, T.H., Guiness, F.E. & Albon, S.D. (1982). Red deer: The behaviour and ecology of two sexes. Chicago, US: University of Chicago Press.

Clutton-Brock, T.H., Iason, G.R. & Guiness, F.E. (1987). Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). Journal of zoology 211: 275-289. https://doi.org/10.1111/j.1469-7998.1987.tb01534.x

Crook, J.H. (1964). The evolution of social organisation and visual communication in the weaver birds (*Ploceinae*). Behaviour, 10, 1–178.

Conrad, L., Clutton-Brock, T.H. & Guiness, F.E. (2000). Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. Animal Behavior, 59, 1049- 1060. https://doi.org/10.1006/anbe.2000.1409

Davies, N. B., Krebs, J. R. & West, S. A. (2012). An introduction to behavioural ecology. Chichester, UK: Wiley-Blackwell Ltd.

De Lisle, S.P. (2019). Understanding the evolution of ecological sex differences: Integrating character displacement and the Darwin- Bateman paradigm. Evolution Letters, 3-5: 434-447. https://doi.org/10.1002/evl3.134

du Toit, J.T. (2005). Sex differences in the foraging ecology of large mammalian herbivores. In K.E. Ruckstuhl & P. Neuhaus (Eds.), Sexual segregation in Vertebrates (pp. 35-52), Cambridge UK: Cambridge University Press.

Eisenberg, J. F. (1966). The social organisation of mammals. Handbook of Zoology, 10, 1-92.

Eisenberg J. F. & McKay, G. M. (1974). Comparison of ungulate adaptations in the new-world and old- world tropical forests with special reference to Ceylon and the rainforests of Central America. In V. Geist & F. Walther (Eds.), The behaviour of ungulates and its relation to management. IUCN Publication new series No. 24, Morges, Switzerland.

Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection and the evolution of mating systems. Science, 197, 215-223.

Estes, R. D. (1974). Social organization of the African bovids. In V. Geist & F. Walther (Eds.) The behaviour of ungulates and its relation to management (pp: 166-205). Vol. I. I.U.C.N., Morges, Switzerland.

Fairbairn, D., Blackenhorn, W. & Székely, T. (2007) Sex, size and gender roles. Evolutionary studies of sexual size dimorphism. Oxford University Press, UK.

Felsenstein, J. (1985). Phylogenesis and comparative method. The American Naturalist, 125, 1-15. https://doi.org/10.1086/284325

Firman, R.C., Rubenstein, D.R., Moran, J.M., Rowe, K.C. & Buzatto, B.A. (2020). Extreme and variable climatic conditions drive the evolution of sociality in Australian rodents. Current Biology 30(4), 691-697. https://doi.org/10.1016/j.cub.2019.12.012

Freckleton, R. P., Harvey, P. H. & Pagel, M. (2002). Phylogenetic Analysis and Comparative Data: A Test and Review of Evidence. American Naturalist, 160, 712-726.

Geist, V. (1966). The evolution of horn- like organs. Behaviour, 27: 175-214. https://doi.org/10.1163/156853966X00155

Geist, V. (1974). On the relationship of social evolution and ecology in ungulates. American Zoologist, 14, 205-220. https://doi.org/10.1093/icb/14.1.205

Ginnett, T.F & Demmet, M.W. (1997). Sex differences in giraffe foraging behavior at two spatial scales. Oecologia, 110, 291-300. https://doi.org/10.1007/s004420050162

Grassi, C. (2002). Sex differences in feeding, high and space use in *Hapalemur griseus*. International Journal of Primatology, 23, 677-693. https://doi.org/10.1023/A:1014934103832

Gonzalez-Voyer, A. & von Hardenberg, A. (2014). An introduction to phylogenetic path analysis. In L.Z. Garamszegi (Ed.), Modern phylogenetic comparative methods and their application in evolutionary biology. (pp. 201-229). Berlin Heidelberg, Germany: Springer- Verlag.

Greenwood, P.J. (1980). Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour, 28, 1140-1162. https://doi.org/10.1016/S0003-3472(80)80103-5

Harvey, P.H. & Pagel, M.D. (1991). The comparative method in evolutionary biology. Oxford, UK: Oxford University Press.

Isvaran, K. (2005). Variation in male mating behaviour within ungulate populations: Patterns and processes. Current Science, 89, 1192-119.

Jaeggi, A.V., Miles, M.I., Festa-Bianchet, M, Shradin, C. & Hayes, L.D. (2020). Variable social organization is ubiquitous in Artiodactyla and probably evolved from pair-living ancestor. Proceedings of the Royal Society London B, 287, 20200035. https://doi.org/10.1098/rspb.2020.0035

Janis, C. M. (1982). Evolution of horns in ungulates: ecology and paleoecology. Biological Reviews, 57, 261-317. https://doi.org/10.1111/j.1469-185X.1982.tb00370.x

Jarman, P.J. (1974). The social organization of antelope in relation to their ecology. Behaviour, 48, 215-266. https://doi.org/10.1163/156853974X00345

Jarman, P. J. & Sinclair, A. R. E. (1979). Feeding strategy and the pattern of resource-partitioning in ungulates. In A.R.E. Sinclair & M. Norton-Griffiths (Eds.), Serengeti: Dynamics of an Ecosystem (pp. 130-163). Chicago, US: University of Chicago Press.

Kleiber, M. (1947). Body size and metabolic rate. Physiological Reviews, 27, 512- 541. https://doi.org/10.1152/physrev.1947.27.4.511

Krause, J. &. Ruxton, G. D. (2002). Living in Groups. Oxford, UK: Oxford University Press.

Lefcheck, J. S. (2016). PIECEWISE SEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution, 7, 573-579. https://doi.org/10.1111/2041-210X.12512

Liker, A., Freckleton, R.P. & Székely, T. (2013). The evolution of sex roles in birds is related to adult sex ratio. Nature Communication 4, 1584. https://doi.org/10.1038/ncomms2600

Lindsay, W.K. (2011). Habitat use, diet choice, and nutritional status in female and male Amboseli elephants. In C.J. Moss, H. Croze & P.C. Lee (Eds.), The Amboseli elephants: a long- term perspective on a long-lived mammal. (pp. 51-73). Chicago, US: University of Chicago Press.

Lukas, D. & Clutton-Brock, T.H. (2013). The evolution of social monogamy in mammals. Science 341(6145), 526-530. https://doi.org/10.1126/science.1238677

Lukas, D. & Clutton-Brock, T.H. (2020). Monotocy and the evolution of plural breeding in mammals. Behavioral Ecology 34(4), 943–949. https://doi.org/10.1093/beheco/araa039

Main, M.B. & du Toit, J.T. (2005). Sex differences in reproductive strategies affect habitat choice in ungulates. In K.E. Ruckstuhl & P. Neuhaus (Eds.) Sexual segregation in Vertebrates (pp. 148-161). Cambridge University Press, Cambrigdge.

Mysterud. A. (2000). The relationship between ecological segregation and sexual body size dimorphism in large herbivores. Oecologia, 124, 40-54. https://doi.org/10.1007/s004420050023

Orme, D. & Freckleton, R. P. (2013). The caper package: comparative analysis of phylogenetics and evolution in R. R package version, 5(2), https://cran.rproject.org/web/packages/caper/vignettes/caper.pdf.

Owen-Smith, N. & Novellie, P. (1982). What should clever ungulates eat? American Naturalist, 119(2), 151-178. https://doi.org/10.1086/283902

Paradis E. (2012). Analysis of phylogenetics and evolution with R (second edition). Springer, New York.

Pérez-Barbería, F.J. & Gordon, I.J. (1998). The influence of molar occlusal surface area on the voluntary intake, digestion, chewing behaviour and diet selection of red deer

(*Cervus elaphus*). Journal of Zoology, 254: 307-16. https://doi.org/10.1111/j.1469-7998.1998.tb00106.x

Pérez-Barbería, F. J., Gordon, I. J. & Pagel, M. (2002). The origin of sexual dimorphism in body size in ungulates. Evolution, 56, 1276-1285. https://doi.org/10.1111/j.0014-3820.2002.tb01438.x

Pérez-Barbería, F.J., Ramsay, S.L., Hooper, R.J., Pérez-Fernández, E., Robertson, A.H.J., Aldezbal, A., Goddart, P. & Gordon, I.J. (2015). The influence of habitats on body size and tooth wear in Scottish red deer (*Cervus elaphus*). Canadian Journal of Zoology, 93, 61-70. https://doi.org/10.1139/cjz-2014-0150

R Core Team. (2016) Version 3.5.3. R: a language and environment for statistical computing. See http://www.r-project.org/

Rubenstein, D.R. & Lovette, I.J. (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. Current Biology 17(16), 1414-1419. https://doi.org/10.1016/j.cub.2007.07.032

Santos, J.C. (2012). Fast molecular evolution associated with high active metabolic rates in poison frogs. Molecular Biology and Evolution, 29, 2001-2018. https://doi.org/10.1093/molbev/mss069

Santos, J.C. & Cannatella, D.C. (2011). Phenotypic integration emerges from aposematism and scale in poison frogs. Proceedings of the National Academy of Sciences of the United States of America, 108, 6175-6180. https://doi.org/10.1073/pnas.1010952108

Schact, R. & Borgerhoff Mulder, M. (2015). Sex ratio effects on reproductive strategies in humans. Royal Society Open Science 2, 1404402. https://doi.org/10.1098/rsos.140402

Schacht, R., Kramer, K.L. Székely, T. & Kappeler, P.M. (2017). Adult sex ratio and reproductive decisions: a critical re-examination of sex differences in human and animal societies. Philosophical Transactions of the Royal Society B 372: 20160309. http://dx.doi.org/10.1098/rstb.2016.0309

Shen, S.F., Emlen, S.T., Koenig, W.D. & Rubenstein, D.R. (2017). The ecology of cooperative breeding behaviour. Ecology Letters 20(6), 708-720. https://doi.org/10.1111/ele.12774

Shi, J., Li, X., Lu, F., Zhuge, H. & Dong, S. (2019). Variation in group size of sympatric wild yak, Tibetan wild ass and Tibetan antelope in Arjin Shan National Nature Reserve of Xinjiang Province, China. Global Ecology and Conservation, 20, e00749. https://doi.org/10.1016/j.gecco.2019.e00749

Shultz, S., Opie, C. & Atkinson, Q. D. (2011). Stepwise evolution of stable sociality in primates. Nature, 479, 219-222. https://doi.org/10.1038/nature10601

Staines, B.W. & Crisp, J.M. (1978). Observations on food quality in Scottish red deer (*Cervus elaphus*) as determined by chemical analysis of rumen content. Journal of Zoology, 185, 253-259. https://doi.org/10.1111/j.1469-7998.1978.tb03325.x

Song, Z., Liker, A., Liu, Y. & Székely, T. Evolution of social organization: phylogenetic analyses of ecology and sexual selection in weavers. American Naturalist, in revision.

Székely, T., Weissing, F.J. & Komdeur, J. (2014). Adult sex ratio variation: implication for breeding system evolution. Journal of Evolutionary Biology 27: 1500-1512. https://doi.org/10.1111/jeb.12415

West, H.E. & Capellini, I. (2016). Male care and life history traits in mammal. Nature Communications 7, 11854. https://doi.org/10.1038/ncomms11854

Wilson, D. E. & Mittermeier, R. A. (2011). Handbook of the Mammals of the Word. Vol. 2. Hoofed Mammals. Barcelona, Spain: Lynx Editions.

Wilson, D. S. (1975). A theory of group selection. Proceedings of the National Academy of Sciences of the United States of America, 72, 143-146.

Winternon, D.J., van Wilgen, N.J. & Venter, J.A. (2020). Investigating the effects of management practice on mammalian co- occurrence along the West Coast of South Africa. PeerJ, 8, 8184. http://doi.org/10.7717/peerj.8184

Wittenberger, J.F. (1981). Animal social behavior. Boston, US: Duxbury Press.

Figure legends

Figure 1. Social evolution in ungulates. (A) An ecological scenario proposed by Jarman (1974), and (B) best-fit model in phylogenetic confirmatory analyses (Fisher's C = 15.689, *df* = 12, $p = 0.206$). We provide path coefficients for each pathway. Width of the arrows indicate the robustness of a particular pathway.

Figure 2. Phylogenetic distribution of ecological and social variables in ungulates. For illustrative purpose, continuous variables were split into binary variables as follows. For body size and group size, we calculated the mean value of these variables, and species were split whether below or above the mean for a given variable. Sexual size dimorphism (SSD) was termed monomorphic if SSD was zero, whereas species with SSD larger than zero were termed male-biased SSD, and species with SSD less than zero were termed female-biased SSD. Note that Tayassuidae represented only on A, since we have no data on any species' mating system from this family (See distribution of variables in S2 supplementary material Table S1 and Fig. S2).

Figure 3. Ecology (habitat type, feeding style) of ungulates in relation to (A, B) body size and (C, D) social organization. See statistics in Table 1.

Figure 4. Group size is related to (A) body size and (B) sexual size dimorphism in ungulates. See statistics in Table 1.

Figure 5. Mating system in relation to (A) group size and (B) sexual size dimorphism in ungulates. See statistics in Table 1.

Table 1: Ecology, body size and social organisation in ungulates using bivariate phylogenetically corrected generalized linear squares models (PGLS). Feeding style, habitat type and mating system were binary variables. Body size provided in kg. Sexual size dimorphism (SSD) was calculated as log_{10} (male body size / female body size). Group size refers to the mean number of individuals per group. Group size and body size were *log*-transformed prior to the analyses. We provide parameter estimates with standard error ($\beta \pm SE$), adjusted R^2, the corresponding t and p values and number of species (N). The diagnostic plots for the models are provided in Supplementary Material Fig. S5.

1. Body size (response variable)

	β ± SE	**adjusted R²**	**t**	***p*-value**	**N**
Feeding style	-0.152 ± 0.061	0.031	-2.4636	0.014	161
Habitat type	0.371 ± 0.076	0.133	4.879	< 0.001	149

2. Group size (response variable)

	β ± SE	**adjusted R²**	**T**	***p*- value**	**N**
Feeding style	-0.385 ± 0.075	0.125	-5.113	< 0.001	176
Habitat type	0.391 ± 0.082	0.119	4.732	< 0.001	159
Body size	0.359 ± 0.063	0.171	5.633	< 0.001	153

3.a Sexual size dimorphism (response variable)

	β ± SE	**adjusted R²**	**t**	***p*- value**	**N**
Group size	0.077 ± 0.015	0.133	4.888	< 0.001	153
Mating system	0.137 ± 0.018	0.343	7.345	< 0.001	102

3.b Mating system (response variable)

	β ±SE	**adjusted R^2**	**t**	***p*- value**	**N**
Group size	0.784 ± 0.091	0.418	8.637	< 0.001	94

Figure 1

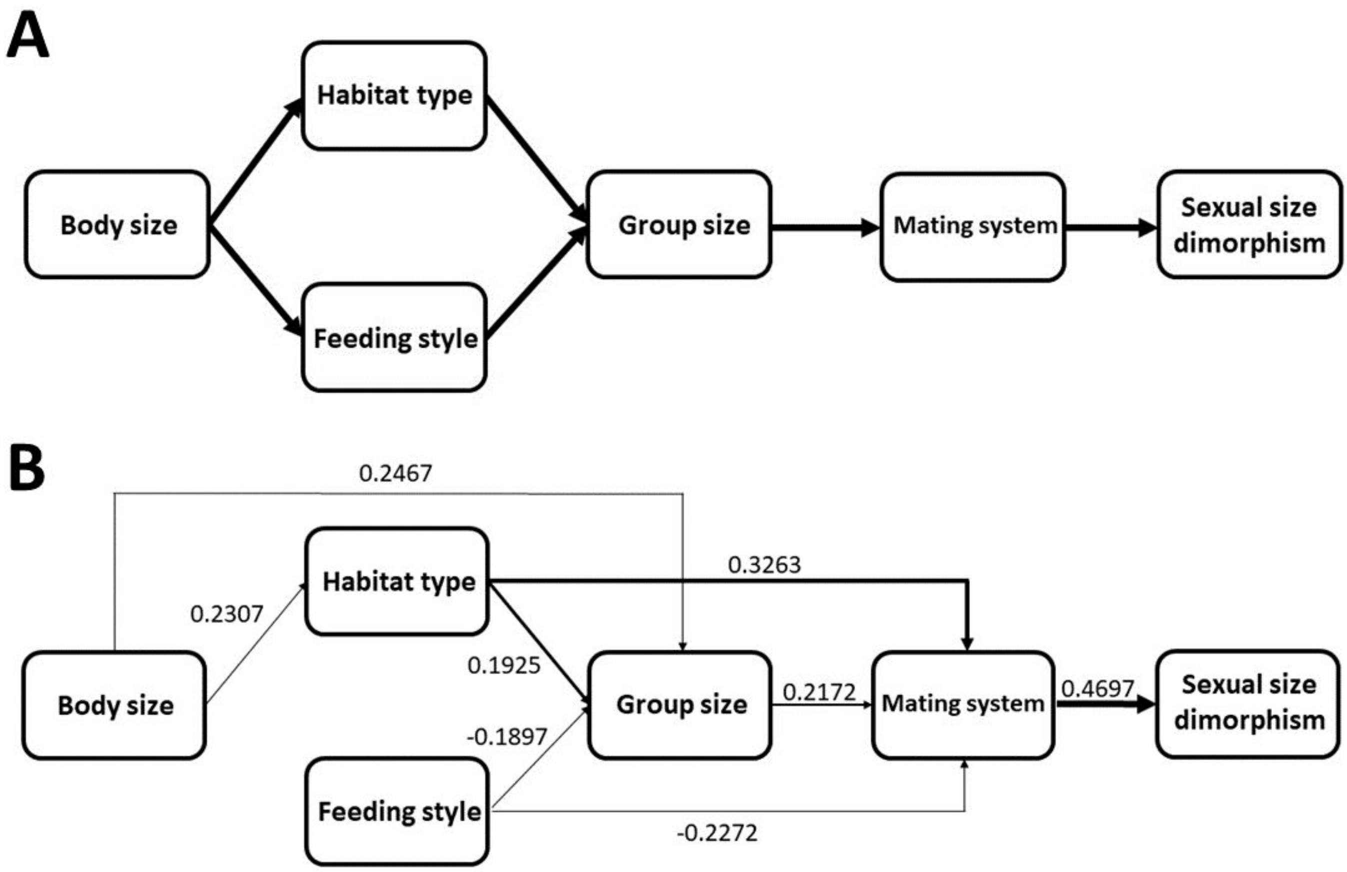
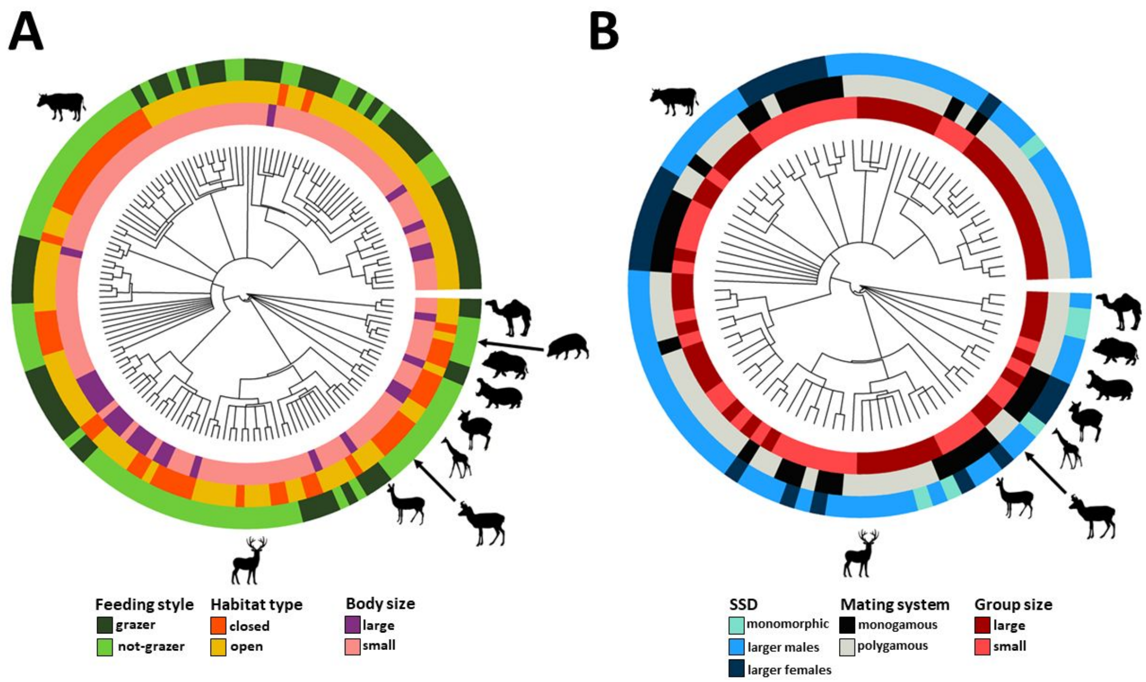
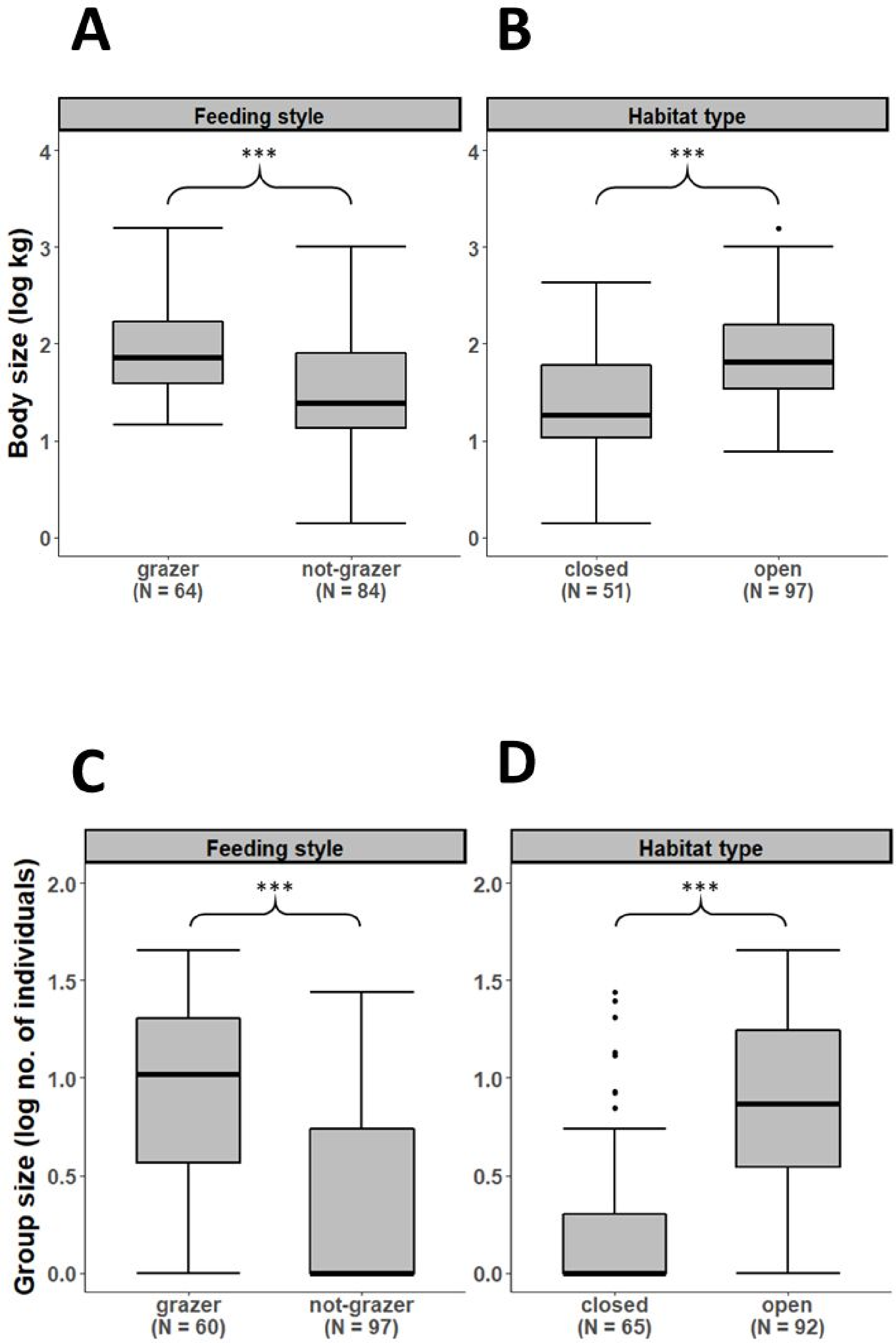

A
Body size
Habitat type
Feeding style
Group size
Mating system
Sexual size dimorphism
B
0.2467
0.2307
Habitat type
0.3263
0.1925
Body size
Group size
0.2172
Mating system
0.4697
Sexual size dimorphism
-0.1897
Feeding style
-0.2272

Figure 2


A
B
Feeding style
grazer
not-grazer
Habitat type
closed
open
Body size
large
small
SSD
monomorphic
larger males
larger females
Mating system
monogamous
polygamous
Group size
large
small

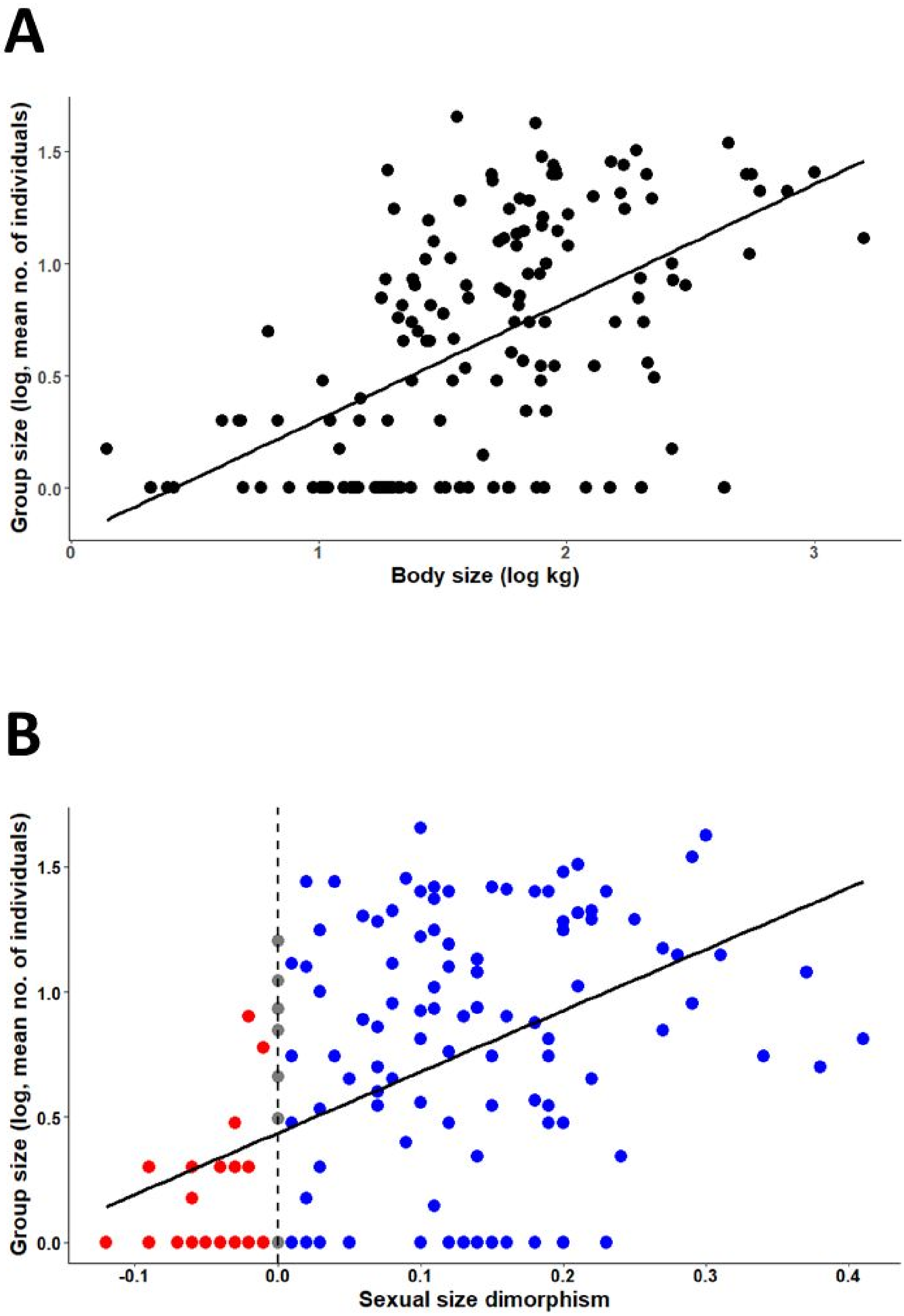
587 Figure 3



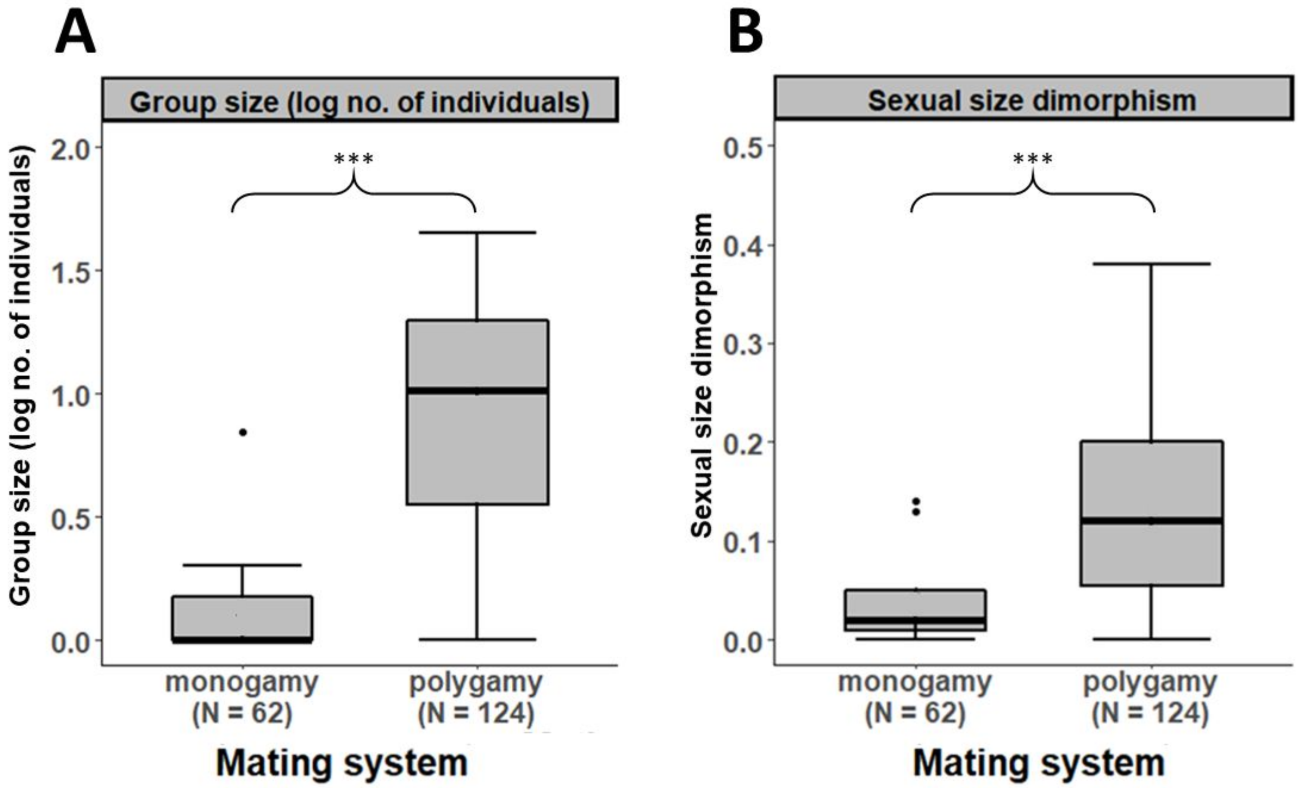
588

589

Figure 4


A
Group size (log, mean no. of individuals)
1.5
1.0
0.5
0.0
0
1
2
3
Body size (log kg)
B
Group size (log, mean no. of individuals)
1.5
1.0
0.5
0.0
-0.1
0.0
0.1
0.2
0.3
0.4
Sexual size dimorphism

592 Figure 5



593

Species	Family	Feeding style_reference
Addax_nasomaculatus	Bovidae	Wilson and Mittermeier 20
Aepyceros_melampus	Bovidae	Wilson and Mittermeier 20
Alcelaphus_buselaphus	Bovidae	Wilson and Mittermeier 20
Alcelaphus_caama	Bovidae	Wilson and Mittermeier 20
Alcelaphus_lichtensteinii	Bovidae	Wilson and Mittermeier 20
Alces_alces	Cervidae	Wilson and Mittermeier 20
Alces_americanus	Cervidae	
Ammodorcas_clarkei	Bovidae	Wilson and Mittermeier 20
Ammotragus_lervia	Bovidae	Wilson and Mittermeier 20
Antidorcas_marsupialis	Bovidae	Wilson and Mittermeier 20
Antilocapra_americana	Antilocapridae	Wilson and Mittermeier 20
Antilope_cervicapra	Bovidae	Wilson and Mittermeier 20
Axis_axis	Cervidae	Wilson and Mittermeier 20
Axis_calamianensis	Cervidae	Wilson and Mittermeier 20
Axis_kuhlii	Cervidae	Wilson and Mittermeier 20
Axis_porcinus	Cervidae	Wilson and Mittermeier 20
Babyrousa_babyrussa	Suidae	Wilson and Mittermeier 20
Babyrousa_bolabatuensis	Suidae	
Babyrousa_celebensis	Suidae	Wilson and Mittermeier 20
Babyrousa_togeanensis	Suidae	Wilson and Mittermeier 20
Damaliscus_hunteri	Bovidae	Wilson and Mittermeier 20
Bison_bison	Bovidae	Wilson and Mittermeier 20
Blastocerus_dichotomus	Cervidae	Wilson and Mittermeier 20
Bos_frontalis	Bovidae	Wilson and Mittermeier 20
Bos_grunniens	Bovidae	Wilson and Mittermeier 20
Bos_javanicus	Bovidae	Wilson and Mittermeier 20
Bos_sauveli	Bovidae	Wilson and Mittermeier 20
Boselaphus_tragocamelus	Bovidae	Wilson and Mittermeier 20
Bubalus_bubalis	Bovidae	Wilson and Mittermeier 20
Bubalus_depressicornis	Bovidae	Wilson and Mittermeier 20
Bubalus_mindorensis	Bovidae	Wilson and Mittermeier 20
Bubalus_quarlesi	Bovidae	Wilson and Mittermeier 20
Budorcas_taxicolor	Bovidae	Wilson and Mittermeier 20
Camelus_bactrianus	Camelidae	Wilson and Mittermeier 20
Camelus_dromedarius	Camelidae	Wilson and Mittermeier 20
Capra_aegagrus	Bovidae	Wilson and Mittermeier 20
Capra_caucasica	Bovidae	Wilson and Mittermeier 20
Capra_falconeri	Bovidae	Wilson and Mittermeier 20
Capra_ibex	Bovidae	Wilson and Mittermeier 20
Capra_nubiana	Bovidae	Wilson and Mittermeier 20
Capra_pyrenaica	Bovidae	Wilson and Mittermeier 20
Capra_sibirica	Bovidae	Wilson and Mittermeier 20
Capra_walie	Bovidae	Wilson and Mittermeier 20
Capreolus_capreolus	Cervidae	Wilson and Mittermeier 20
Capreolus_pygargus	Cervidae	Wilson and Mittermeier 20
Naemorhedus_crispus	Bovidae	Wilson and Mittermeier 20
Capricornis_milneedwardsii	Bovidae	Wilson and Mittermeier 20
Capricornis_rubidus	Bovidae	Wilson and Mittermeier 20
Naemorhedus_sumatraensis	Bovidae	Wilson and Mittermeier 20
Naemorhedus_swinhoei	Bovidae	Wilson and Mittermeier 20
Capricornis_thar	Bovidae	Wilson and Mittermeier 20
Catagonus_wagneri	Tayassuidae	Wilson and Mittermeier 20

Cephalophus_adersi	Bovidae	Wilson and Mittermeier 20
Cephalophus_brookei	Bovidae	Wilson and Mittermeier 20
Cephalophus_callipygus	Bovidae	Wilson and Mittermeier 20
Cephalophus_dorsalis	Bovidae	Wilson and Mittermeier 20
Cephalophus_jentinki	Bovidae	Wilson and Mittermeier 20
Cephalophus_leucogaster	Bovidae	Wilson and Mittermeier 20
Cephalophus_natalensis	Bovidae	Wilson and Mittermeier 20
Cephalophus_niger	Bovidae	Wilson and Mittermeier 20
Cephalophus_nigrifrons	Bovidae	Wilson and Mittermeier 20
Cephalophus_ogilbyi	Bovidae	Wilson and Mittermeier 20
Cephalophus_rufilatus	Bovidae	Wilson and Mittermeier 20
Cephalophus_silvicultor	Bovidae	Wilson and Mittermeier 20
Cephalophus_spadix	Bovidae	Wilson and Mittermeier 20
Cephalophus_zebra	Bovidae	Wilson and Mittermeier 20
Cervus_canadensis	Cervidae	Wilson and Mittermeier 20
Cervus_elaphus	Cervidae	Wilson and Mittermeier 20
Cervus_nippon	Cervidae	Wilson and Mittermeier 20
Cervus timorensis	Cervidae	Wilson and Mittermeier 20
Connochaetes_gnou	Bovidae	Wilson and Mittermeier 20
Connochaetes_taurinus	Bovidae	Wilson and Mittermeier 20
Dama_dama	Cervidae	Wilson and Mittermeier 20
Damaliscus_korrigum	Bovidae	Wilson and Mittermeier 20
Damaliscus_lunatus	Bovidae	Wilson and Mittermeier 20
Damaliscus_pygargus	Bovidae	Wilson and Mittermeier 20
Dorcatragus_megalotis	Bovidae	Wilson and Mittermeier 20
Elaphodus_cephalophus	Cervidae	Wilson and Mittermeier 20
Gazella_rufifrons	Bovidae	Wilson and Mittermeier 20
Gazella_thomsonii	Bovidae	Wilson and Mittermeier 20
Gazella_arabica	Bovidae	
Gazella_bennettii	Bovidae	Wilson and Mittermeier 20
Gazella_cuvieri	Bovidae	Wilson and Mittermeier 20
Gazella_dorcas	Bovidae	Wilson and Mittermeier 20
Gazella_erlangeri	Bovidae	Wilson and Mittermeier 20
Gazella_gazella	Bovidae	Wilson and Mittermeier 20
Gazella_leptoceros	Bovidae	Wilson and Mittermeier 20
Gazella_spekei	Bovidae	Wilson and Mittermeier 20
Gazella_subgutturosa	Bovidae	Wilson and Mittermeier 20
Giraffa_camelopardalis	Giraffidae	Wilson and Mittermeier 20
Hemitragus_hylocrius	Bovidae	Wilson and Mittermeier 20
Hemitragus_jayakari	Bovidae	Wilson and Mittermeier 20
Hemitragus_jemlahicus	Bovidae	Wilson and Mittermeier 20
Hexaprotodon_liberiensis	Hippopotamidae	Wilson and Mittermeier 20
Hippocamelus_antisensis	Cervidae	Wilson and Mittermeier 20
Hippocamelus_bisulcus	Cervidae	Wilson and Mittermeier 20
Hippopotamus_amphibius	Hippopotamidae	Wilson and Mittermeier 20
Hippotragus_equinus	Bovidae	Wilson and Mittermeier 20
Hippotragus_niger	Bovidae	Wilson and Mittermeier 20
Hydropotes_inermis	Cervidae	Wilson and Mittermeier 20
Hyemoschus_aquaticus	Tragulidae	Wilson and Mittermeier 20
Hylochoerus_meinertzhageni	Suidae	Wilson and Mittermeier 20
Kobus_ellipsiprymnus	Bovidae	Wilson and Mittermeier 20
Kobus_kob	Bovidae	Wilson and Mittermeier 20
Kobus_leche	Bovidae	Wilson and Mittermeier 20

Kobus_megaceros	Bovidae	Wilson and Mittermeier 20
Kobus_vardonii	Bovidae	Wilson and Mittermeier 20
Lama_guanicoe	Camelidae	Wilson and Mittermeier 20
Litocranius_walleri	Bovidae	Wilson and Mittermeier 20
Madoqua_guentheri	Bovidae	Wilson and Mittermeier 20
Madoqua_kirkii	Bovidae	Wilson and Mittermeier 20
Madoqua_piacentinii	Bovidae	
Madoqua_saltiana	Bovidae	Wilson and Mittermeier 20
Mazama_americana	Cervidae	Wilson and Mittermeier 20
Mazama_bororo	Cervidae	Wilson and Mittermeier 20
Mazama_bricenii	Cervidae	
Mazama_chunyi	Cervidae	Wilson and Mittermeier 20
Mazama_gouazoupira	Cervidae	Wilson and Mittermeier 20
Mazama_nana	Cervidae	Wilson and Mittermeier 20
Mazama_pandora	Cervidae	Wilson and Mittermeier 20
Mazama_rufina	Cervidae	Wilson and Mittermeier 20
Mazama_temama	Cervidae	Wilson and Mittermeier 20
Moschiola_meminna	Tragulidae	
Moschus_anhuiensis	Moschidae	
Moschus_berezovskii	Moschidae	Wilson and Mittermeier 20
Moschus_chrysogaster	Moschidae	Wilson and Mittermeier 20
Moschus_cupreus	Moschidae	Wilson and Mittermeier 20
Moschus_fuscus	Moschidae	Wilson and Mittermeier 20
Moschus_leucogaster	Moschidae	Wilson and Mittermeier 20
Moschus_moschiferus	Moschidae	Wilson and Mittermeier 20
Muntiacus_atherodes	Cervidae	Wilson and Mittermeier 20
Muntiacus_crinifrons	Cervidae	Wilson and Mittermeier 20
Muntiacus_feae	Cervidae	Wilson and Mittermeier 20
Muntiacus_gongshanensis	Cervidae	Wilson and Mittermeier 20
Muntiacus_muntjak	Cervidae	Wilson and Mittermeier 20
Muntiacus_puhoatensis	Cervidae	
Muntiacus_putaoensis	Cervidae	Wilson and Mittermeier 20
Muntiacus_reevesi	Cervidae	Wilson and Mittermeier 20
Muntiacus_rooseveltorum	Cervidae	Wilson and Mittermeier 20
Muntiacus_truongsonesnsis	Cervidae	Wilson and Mittermeier 20
Muntiacus_vuquangensis	Cervidae	Wilson and Mittermeier 20
Naemorhedus_baileyi	Bovidae	Wilson and Mittermeier 20
Naemorhedus_caudatus	Bovidae	Wilson and Mittermeier 20
Naemorhedus_goral	Bovidae	Wilson and Mittermeier 20
Naemorhedus_griseus	Bovidae	Wilson and Mittermeier 20
Gazella_dama	Bovidae	Wilson and Mittermeier 20
Gazella_granti	Bovidae	Wilson and Mittermeier 20
Gazella_soemmerringii	Bovidae	Wilson and Mittermeier 20
Neotragus_batesi	Bovidae	Wilson and Mittermeier 20
Neotragus_moschatus	Bovidae	Wilson and Mittermeier 20
Neotragus_pygmaeus	Bovidae	Wilson and Mittermeier 20
Odocoileus_hemionus	Cervidae	Wilson and Mittermeier 20
Odocoileus_virginianus	Cervidae	Wilson and Mittermeier 20
Okapia_johnstoni	Giraffidae	Wilson and Mittermeier 20
Oreamnos_americanus	Bovidae	Wilson and Mittermeier 20
Oreotragus_oreotragus	Bovidae	Wilson and Mittermeier 20
Oryx_dammah	Bovidae	Wilson and Mittermeier 20
Oryx_gazella	Bovidae	Wilson and Mittermeier 20

Oryx_leucoryx	Bovidae	Wilson and Mittermeier 20
Ourebia_ourebi	Bovidae	Wilson and Mittermeier 20
Ovibos_moschatus	Bovidae	Wilson and Mittermeier 20
Ovis_ammon	Bovidae	Wilson and Mittermeier 20
Ovis_canadensis	Bovidae	Wilson and Mittermeier 20
Ovis_dalli	Bovidae	Wilson and Mittermeier 20
Ovis_nivicola	Bovidae	Wilson and Mittermeier 20
Ozotoceros_bezoarticus	Cervidae	Wilson and Mittermeier 20
Pantholops_hodgsonii	Bovidae	Wilson and Mittermeier 20
Pecari_tajacu	Tayassuidae	Wilson and Mittermeier 20
Pelea_capreolus	Bovidae	Wilson and Mittermeier 20
Phacochoerus_aethiopicus	Suidae	
Phacochoerus_africanus	Suidae	Wilson and Mittermeier 20
Cephalophus_maxwellii	Bovidae	Wilson and Mittermeier 20
Cephalophus_monticola	Bovidae	Wilson and Mittermeier 20
Potamochoerus_larvatus	Suidae	Wilson and Mittermeier 20
Potamochoerus_porcus	Suidae	Wilson and Mittermeier 20
Procapra_gutturosa	Bovidae	Wilson and Mittermeier 20
Procapra_picticaudata	Bovidae	Wilson and Mittermeier 20
Procapra_przewalskii	Bovidae	Wilson and Mittermeier 20
Cervus_albirostris	Cervidae	Wilson and Mittermeier 20
Pseudois_nayaur	Bovidae	Wilson and Mittermeier 20
Pseudois_schaeferi	Bovidae	Wilson and Mittermeier 20
Pseudoryx_nghetinhensis	Bovidae	Wilson and Mittermeier 20
Pudu_mephistophiles	Cervidae	Wilson and Mittermeier 20
Pudu_puda	Cervidae	Wilson and Mittermeier 20
Rangifer_tarandus	Cervidae	Wilson and Mittermeier 20
Raphicerus_campestris	Bovidae	Wilson and Mittermeier 20
Raphicerus_melanotis	Bovidae	Wilson and Mittermeier 20
Raphicerus_sharpei	Bovidae	Wilson and Mittermeier 20
Redunca_arundinum	Bovidae	Wilson and Mittermeier 20
Redunca_fulvorufula	Bovidae	Wilson and Mittermeier 20
Redunca_redunca	Bovidae	Wilson and Mittermeier 20
Cervus_duvaucelii	Cervidae	Wilson and Mittermeier 20
Cervus_eldii	Cervidae	Wilson and Mittermeier 20
Rupicapra_pyrenaica	Bovidae	Wilson and Mittermeier 20
Rupicapra_rupicapra	Bovidae	Wilson and Mittermeier 20
Cervus_alfredi	Cervidae	Wilson and Mittermeier 20
Cervus_mariannus	Cervidae	Wilson and Mittermeier 20
Cervus_timorensis	Cervidae	Wilson and Mittermeier 20
Cervus_unicolor	Cervidae	Wilson and Mittermeier 20
Saiga_borealis	Bovidae	Wilson and Mittermeier 20
Saiga_tatarica	Bovidae	Wilson and Mittermeier 20
Sus_ahoenobarbus	Suidae	Wilson and Mittermeier 20
Sus_barbatus	Suidae	Wilson and Mittermeier 20
Sus_cebifrons	Suidae	Wilson and Mittermeier 20
Sus_celebensis	Suidae	Wilson and Mittermeier 20
Sus_oliveri	Suidae	
Sus_philippensis	Suidae	Wilson and Mittermeier 20
Sus_salvanius	Suidae	Wilson and Mittermeier 20
Sus_scrofa	Suidae	Wilson and Mittermeier 20
Sus_verrucosus	Suidae	Wilson and Mittermeier 20
Sylvicapra_grimmia	Bovidae	Wilson and Mittermeier 20

Syncerus_caffer	Bovidae	Wilson and Mittermeier 20
Taurotragus_derbianus	Bovidae	Wilson and Mittermeier 20
Taurotragus_oryx	Bovidae	Wilson and Mittermeier 20
Tayassu_pecari	Tayassuidae	Wilson and Mittermeier 20
Tetracerus_quadricornis	Bovidae	Wilson and Mittermeier 20
Tragelaphus_angasii	Bovidae	Wilson and Mittermeier 20
Tragelaphus_buxtoni	Bovidae	Wilson and Mittermeier 20
Tragelaphus_eurycerus	Bovidae	Wilson and Mittermeier 20
Tragelaphus_imberbis	Bovidae	Wilson and Mittermeier 20
Tragelaphus_scriptus	Bovidae	Wilson and Mittermeier 20
Tragelaphus_spekii	Bovidae	Wilson and Mittermeier 20
Tragelaphus_strepsiceros	Bovidae	Wilson and Mittermeier 20
Tragulus_javanicus	Tragulidae	Wilson and Mittermeier 20
Tragulus_kanchil	Tragulidae	Wilson and Mittermeier 20
Tragulus_napu	Tragulidae	Wilson and Mittermeier 20
Tragulus_nigricans	Tragulidae	Wilson and Mittermeier 20
Tragulus_versicolor	Tragulidae	
Tragulus_williamsoni	Tragulidae	Wilson and Mittermeier 20
Vicugna_vicugna	Camelidae	Wilson and Mittermeier 20

Habitat type_reference	Mating system_reference	Group size_reference
Wilson and Mittermeier 2011		East 1990
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Skinner and Chimimba 2005
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Skinner and Chimimba 2005
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Chubbs and Shafer 1997
Wilson and Mittermeier 2011		East 1988
Wilson and Mittermeier 2011		Cassinello 2000
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Nowak and Paradiso 1983
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mallon 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
)11		Wemmer 1998
Wilson and Mittermeier 2011		Semiadi et al. 2005
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Macdonald et al. 2008
Wilson and Mittermeier 2011		Leus et al. 2016
Wilson and Mittermeier 2011		Macdonald et al. 2016
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Nowak and Paradiso 1983
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Leslie and Shaller 2009
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Nowak and Paradiso 1983
Wilson and Mittermeier 2011		Nowak and Paradiso 1983
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mallon 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Burton et al. 2016a
Wilson and Mittermeier 2011		Custodio et al. 1996
Wilson and Mittermeier 2011		Burton et al. 2016b
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Neas and Hoffmann 1987, S
Wilson and Mittermeier 2011		Reading et al. 1999
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Nickolson and Husband 199
)11		Baskin and Danell 2003
Wilson and Mittermeier 2011		Baskin and Danell 2003
Wilson and Mittermeier 2011		Aulagnier et al. 2008
Wilson and Mittermeier 2011		Aulagnier et al. 2008
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Habibi 1996
Wilson and Mittermeier 2011		Perez et al. 1994
Wilson and Mittermeier 2011		Fedosenko and Blank 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Ejigu et al. 2015
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011	Tokida 2008 IUCn report	Hutchins et al. 2003
Wilson and Mittermeier 2011		Vongkhamheng et al. 2013
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Nowak and Paradiso 1983,
Wilson and Mittermeier 2011		Chiang 2008
Wilson and Mittermeier 2011		Bhattacharya et al. 2012, Gi
)11		Hutchins et al. 2003

Wilson and Mittermeier 2011		East 1988
Wilson and Mittermeier 2011		Kingdon and Hoffmann 201
Wilson and Mittermeier 2011		Kingdon 2015
Wilson and Mittermeier 2011		Kingdon and Hoffmann 201
Wilson and Mittermeier 2011		Kingdon and Hoffmann 201
Wilson and Mittermeier 2011		Skinner and Chimimba 200
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Skinner and Chimimba 200
Wilson and Mittermeier 2011		Kingdon and Hoffmann 201
Wilson and Mittermeier 2011		Kingdon and Hoffmann 201
Wilson and Mittermeier 2011		Kingdon and Hoffmann 201
Wilson and Mittermeier 2011		East 1990
Wilson and Mittermeier 2011		East 1988
Wilson and Mittermeier 2011		Kingdon and Hoffmann 201
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011		Strushaker 1967
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Vrahimis 1994
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Skinner and Chimimba 200
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Feldhamer et al. 1988
)11		Jewell 1972, Grant et al. 19
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011		Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988, Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
)11		East 1990
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
		Wronski 2013
)11		Dookia and Jakher 2013
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011		East 1990
)11		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Mallon 2001
)11		East 1990, Mallon 2001
)11		Kingdon 2015
Wilson and Mittermeier 2011		Kingswood and Blank 1996
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Green 1978
Wilson and Mittermeier 2011		Oliver 1993
Wilson and Mittermeier 2011		Mertk 1985
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Karstad and Hudson 1986
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988, 1990
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015

)11		East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
)11		East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hendrichs 1975
		Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
)11		Wilson and Mittermeier 20
		Wilson and Mittermeier 20
)11		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
)11		Hutchins et al. 2003
)11		Wilson and Mittermeier 20
)11		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
)11		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Hutchins et al. 2003
)11		Wilson and Mittermeier 20
)11		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mead 1989, Wilson and Mi
)11		Duckworth et al 2008b
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
)11		East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011		Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003, Kingdo
Wilson and Mittermeier 2011		Risenhoover and Bailey 198
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011		Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988

Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Stewart 1963, Wilson and M
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Stewart 1963, Wilson and M
011		Stewart 1963, Wilson and M
Wilson and Mittermeier 2011		Shakelton 1985
Wilson and Mittermeier 2011		Bowyer and Leslie 1992
011		Baskin and Danell 2003, Ha
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mallon 2001
Wilson and Mittermeier 2011		Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Halsdorf 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
011		Kingdon 2015
Wilson and Mittermeier 2011		Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mallon 2001
Wilson and Mittermeier 2011		Mallon 2001
Wilson and Mittermeier 2011	antelopes IUCN report	Lei et al. 2001
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wang and Hoffmann 1987
Wilson and Mittermeier 2011		Wang and Hoffmann 1987,
Wilson and Mittermeier 2011		Mallon 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011		Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Skinner and Chimimba 200
Wilson and Mittermeier 2011		East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Sharma et al. 2013
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Aung et al. 2001
Wilson and Mittermeier 2011		Pépin and Gerard 2008
Wilson and Mittermeier 2011	Pérez-Barbería et al. 2002	Wilson and Mittermeier 20
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
011		Wiles et al. 1999
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Leslie 2011
011		
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		
011		Oliver 1993
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
011		Oliver 1993
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Oliver 1993
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Oliver 1993
Wilson and Mittermeier 2011		Oliver 1993
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988

Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	
Wilson and Mittermeier 2011		East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Mallon 2001
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Kingdon 2015
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011		East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	East 1988
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Hutchins et al. 2003
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011		
Wilson and Mittermeier 2011		Wilson and Mittermeier 20
Wilson and Mittermeier 2011	Pérez-Barbería et al.. 2002	Gordon 2009

Male body size_reference	Female body size_reference
Bro-Jørgensen 2007a	Bro-Jørgensen 2007a
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007a	Bro-Jørgensen 2007a
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Pérez-Barbería and Gordon 2000	Pérez-Barbería and Gordon 2000
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
O'Gara1990	O'Gara1990
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Kays and Wilson 2009	Corti et al. 2010
Pérez-Barbería and Gordon 2000	Pérez-Barbería and Gordon 2000
Bro-Jørgensen 2007a	Bro-Jørgensen 2007a
Bro-Jørgensen 2007a	Bro-Jørgensen 2007a
Pérez-Barbería and Gordon 2000	Pérez-Barbería and Gordon 2000
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007a	Bro-Jørgensen 2007a
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Pérez-Barbería and Gordon 2000	Pérez-Barbería and Gordon 2000
92	
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Weigl 2005	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Pérez-Barbería and Gordon 2000	Pérez-Barbería and Gordon 2000
Greaves 1990	
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007a	Bro-Jørgensen 2007a
iri et al. 2011	

Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
.3	
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007a	Bro-Jørgensen 2007a
Pérez-Barbería and Gordon 2000	Pérez-Barbería and Gordon 2000
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
Bro-Jørgensen 2007b	Bro-Jørgensen 2007b
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11	
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Aulagnier, S., A. Kranz, S. Lovari, T. Jdeidi, M. Masseti, I. Nader, K. de Smet and F. Cuzin. 2008. Capra ibe
Aung, M., W.J. McShea, S.Htung, A. Than, T.M. Soe, S. Monfort and C. Wemmer. 2001. Ecology and soci
Baskin, L. and K. Danell. 2003. Ecology of ungulates. A handbook of species in eastern Europe and centr
Bhattacharya, T., T. Bashir, K. Poudyal, S. Sathyakumar and G.H. Saha. 2012. Distribution, occupany and
Bowyer, R.T. and D.M. Leslie. 1992. Ovis dalli. Mammalian Species 393:1-7.
Bro-Jørgensen, J. 2007a. Dense habitats selecting for small body size: a comparative study on bovids. Oi
Bro-Jørgensen, J., 2007b. The intensity of sexual selection predicts weapon size in male bovids. Evolutio
Burton, J., P. Wheeler and A. Mustari. 2016a. Bubalus depressicornis. The IUCN Red list of Threatened S
Burton, J., P. Wheeler and A. Mustari. 2016b. Bubalus quarlesi. The IUCN Red List of Threatened Species
Cassinello, J. 2000. Ammotragus free-ranging population in the south-east of Spain: a necessary first acc
Chiang, P.J., K.J-c. Pei. 2008. Capricornis swihoei. The IUCN Red List of Threatened Species 2008: e.T381
Chubs, T.E. and J.A. Schaefer. 1997. Population growth of moose, Alces alces, in labrador. Canadian Fiel
Cooke, A.S., P. Green and N.G. Chapman. 1996. Mortality in a feral population of muntjac Muntiacus ree
Corti, P., H.U. Wittmer and M. Festa-Bianchet. 2010. Dynamics of a small population of endangered hue
CRU database: http://www.cru.uea.ac.uk/;version 3.10.01
Custodio, C.C., M.V. Lepiten and L.R. Heaney. 1996. Bubalus midorensis. Mammalian Species 520: 1-5.
Dookia, S. and G.R. Jakher. 2013. Social organization and population dynamics of indian gazelle (Gazella
Duckworth, J.W., R. Steinmetz and C. Rattanawat. 2008b. Naemorhedus griseus. The IUCN Red List of Th
Duckworth, J.W., R. Steinmetz and J. MacKinnon. 2008a. Capricornis sumatraensis. The IUCN Red List of
East, R. ed. 1990. Antelopes: Global Survey and regional action plans.Part 3. West and Central Africa
East, R.(ed). 1988. Antelopes: Global survey and regional action plans. Part 1: East and Northeast Africa
Ejigu, D., A. Bekele and J.-M. Lernould. 2015. Habitat preference of the endangered Ethiopian walia ibe
Fedosenko, A.K. and D.A. Blank. 2001. Capra sibirica. Mammalian Species, 675:1-13.
Feldhamer, G.A., K.C. Farris-Renner and C.M. Barker. 1988. Dama dama. Mammalian Species 317:1-8.
Giri, S., A. Aryal, R.K. Koirala, B. Adhikari and D. Raubenheimer. 2001. Feeding ecology and distribution
Gordon, I.J. (ed). 2009. The vicuna: The theory and practice of community based willife management. S
Grant, J.W.A., C.A. Chapman and K.S. Richardson. 1992. Defended versus undefended range size of carn
Greaves, N. 1990. When hippo was hairy: and other tales from Africa. Lutterworth Press, Cambridge.
Green, M.J.B. 1978. The ecology and feeding behaviour of himalayan the (Hemitragus jemalihicus) in th
Habibi, K. 1997. Group dynamics of the Nubian ibex (Capra ibex nubiana) in the Tuwayiq Canyons, Saudi
Halsdorf, S.A. 2002. Die vrteilung von warzenschweinen ineiner durch viehbeweidung modifizieren küst
Harris, R.B. and K. Tsytsulina. 2008. Ovis nivicola. The IUCN Red List of Threatened Species 2008: e.T157
Hellgren, E.C., R.L. Lochmiller and W.E. Grant. 1984. Demographic, morphologic and reproductive statu
Hendrichs, H. 1975. Changes in population of dikdik, Madoqua (Rhynchotragus) kirki (Günther 1880). Ze
Hutchins, M., D.G. Kleiman, V. Geist and M.C. McDade (eds). 2003. Grizmek's animal life encyclopedia, 2
Jewell, P.A. 1972. Social organisation and movements of topi (Damaliscus korrigum) during the rut, at Is
Jiménez, J.E. 2010. The southern pudu (Pudu puda). Pp: 140-150 *in* S. González, J.M. Barbanti (eds) Neo
Karstad, E.L. and R.J. Hudson. 1986. Social organization and communication of riverine hippopotami in s
Kays, R.W. and D.E. Wilson (eds). 2009. Mammals of north America. Princeton University Press, Oxfords
Kingdon, J. 2015. The Kingdon field guide to African mammals, 2nd edition. Bloomsbury Publishing Plc. I
Kingdon, J. and M. Hoffmann (eds). 2013. Mammals of Africa, Vol. 6: Pigs, Hippopotamuses, Chevrotain,
Kingswood, S.C. and D.A. Blank. 1996. Gazella subgutturosa. Mammalian Species 518:1-10.
Lei, R., Z. Jiang and B. Liu. 2001.Group pattern and social segregation in Przewalski's gazelle (Procapra p
Leslie, D.M. 2011. Rusa unicolor. Mammalian Species 43(871):1-30.
Leslie, D.M. and G.B. Schaller. 2009. Bos grunniens and Bos mutus. Mammalian Species 836:1-17.
Leus, K., Macdonald K., J. Burton and I. Rejeki. 2016. Babyrousa celebensis. The IUCN Red List of Threate
Lüpold, S., J.L. Tomkins, L.W. Simmons and J.L. Fitzpatrick. 2014. Female monopolization mediates the r
Macdonald, A.A., J. Burton and K. Leus. 2008. Babyruossa babyroussa. The IUCN Red List of Threatened
Macdonald, A.A., K. Leus, I. Masaaki and J. Burton. 2016. Babyrousa togeanensis. The IUCN Red List of T
Mallon, D.P. and S.C. Kingswood (eds). 2001. Antelopes. Part 4: North Africa, the Middle East and Asia.
Marshal, J.P. 2016. Survival estimation of a cryptic antelope via photographic capture–recapture. Africa
Mead, J. 1989. Nemorhaedus goral. Mammalian Species 335:1-5.

Merkt, J.R. 1985. Social structure of Andean deer (Hippocamelus antisensis) in southern Peru. Master th
Mitchell, T.D. and P. D. Jones. 2005. An improved method of constructing a database of monthly climate
Neas, J.F. and R.S. Hoffmann. 1987. Budorcas taxicolor. Mammalian Species 277:1-7.
Nicholson, M.C. and T. Husband. 1992. Diurnal behavior of the agrimi, Capra aegurus. Journal of Mamm
Nowak, R.M. and J.L. Paradiso (eds). 1983. Walker's mammals of the world, 4th edition, Vol 1. The Johns
O'Gara, B.W. 1990. The Pronghorn (*Antilocapra americana*). In: Bubenik G.A. and Bubenik A.B. (eds) Hor
Oliver, W.L.R. (ed). 1993. Pigs, peccaries and hippos. International Union for Conservation of Nature and
Owen-Smith, R.N. (ed). 1988. Megaherbivores: The influence of very large body size on ecology. Cambri
Pépin, D. and J.-F. Gerard. 2008. Group dynamics and local population density dependence of group size
Pérez, J.M., J.E. Granados and R.C. Soriguer. 1994. Population dynamic of the Spanish ibex Capra pyrena
Pérez. Barbería, F.J. and I.J. Gordon. 2000. Differences in body mass and oral morphology between sexe
Reading, R.P., H. Mix, B. Lhagvasuren and E.S. Blumer. 1999. Status of wild Bactrian camels and other la
Risenhoover, K.L. and J.A. Bailey. 1985. Relationship between group size, feeding time and agonistic beh
Ruckstuhl, K.E. and P. Neuhaus. 2002. Sexual segregation in ungulates: a comparative test of three hypo
Saether, B.-E. and J. Gordon. 1994. The adaptive significance of reproductive strategies in ungulates. Pro
Saha, G.K and S. Mazumdar (eds). 2017. Wildlife biology: an indian perspective. PHI Learning Private Lim
Saunders, G. and S. McLeod. 1999. Predicting home range size from the body mass or population densit
Schaller, G. B. 1967. The Deer and the Tiger – A Study of Wildlife in India. University Chicago Press, Chica
Semiadi, G., J.W. Duckworth and R. Timmins. 2015. Axis khulii. The IU
Shackleton, D.M. (ed). 1997. Wild sheep and goats and their relatives. IUCN, Gland, Switzerland.
Shackleton, D.M. 1985. Ovis canadensis. Mammalian Species 230:1-9.
Sharma, B.K., S. Kulshreshtha and A.R. Rahmani. 2013. Faunal heritage of Rajasthan, India. Springer Scie
Skinner, J.D. and C.T. Chimimba (eds). 2005. The mammals of the Southern African Subregion. Cambridg
Song, Y.-L., A.T. Smith and J. MacKinnon. 2008. Budorcas taxicolor. The IUCN Red List of Threatened Spe
Stewart, D.R.M. 1963. The Arabian oryx (Oryx leuroryx Pallas). East African Wildlife Journal 1:103-117.
Struhsaker, T.T. 1967. Behavior of elk (Cervus canadensis) during rut. Zeitschrift für Tierpsycho, 24:80-1
Vongkhamheng, C., A. Johnson and M.E. Sunquist. 2013. A baseline survey of ungulate abundance and d
Vrahimis, S. and O.B. Kok. 1994. Notes on the diurnal activity of early post-natal black wildebeest calves
Wang, X. and R.S. Hoffmann. Pseudois nayaur and Pseudois schaeferi. Mammalian Species 278:1-6.
Weigl, R. 2005. Longevity of mammals in captivity from the Living collections of the world 21. Schweizer
Wemmer, C. 1998. Deer: Status survey and conservation action plan. IUCN/SSC Deer specialist group. IU
Wiles, G.J., D.W. Buden and D.J. Worthington. 1999. History of introduction, population status and man
Wilson, D. E. and R. A. Mittermeier. 2011. Handbook of the Mammals of the Word. Vol. 2. Hoofed Mam
Wronski, T. 2013. Population development of Arabian gazelles, Gazella arabica, on the Farasan Islands, S

:x. The IUCN Red List of Threatened Species 2008: e.T42397A10695445.http://dx.doi.org/10.2305/IUCN.
al organization of a tropical deer (Cervus eldi thamin). Journal of Mammology 82(3):836-847.
al Asia. Springer- Verlag Berlin Heildelberg GmbH, New York.
activity patterns of goral (Nemorhaedus goral) and serow (Capricornis thar) in Khangchendzonga Biospl

ikos 117:729-737.
n, 61(6):1316-1326.
species 2016: e.T3126A46364222. http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T3126A46364222.en
s 2016: e.T3128A46364433. http://dx.doi.org/10.2305/IUCN.UK.2016-2.RLTS.T3128A46364433.en
count. Biodiversity and Conservation 9:887-900.
.0A10096148.http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T3810A10096148.en
d Naturalist 11(2): 238-242.
evesi in England. Acta Theriologica 41(3):277-286.
emul deer (Hippocamelus bisulcus) in Chilean Patagonia. Journal of Mammalogy, 91(3):690-697.

bennettii) in Thar Desert of Rajasthan, India. Tiger Paper 40(1): 5-14.
hreatened Species 2008: e.T14303A4430834.http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T14303A44
f Threatened Species 2008: e.T3812A10099434.http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T3812A1(

x (Capra walie) in the Simien Mountains National Park, Ethiopia. Animal Biodiversity and Conservation, 3

of Himalayan serow (Capricornis thar) in Annapurna Conservation Area, Nepal. World Journal of Zoology
pringer Science+Business Media, New York.
ivores, ungulates and primates. Behavioral Ecology and Sociobiology 31(3):149-161.

e Langtang valley, Nepal. Durham theses, Durham University: http://etheses.dur.ac.uk/8982/
i Arabia. Journal of Zoology 241:791-801.
tensavanne Tansanias. Master thesis, Eidgenössische Technische Hochschule, Zürich.
'40A5076357. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T15740A5076357.en
s of a herd of collared peccaries (Tayassu tajacu) in south Texas. American Midland Naturalist 112(2):402
eitschrift für Tierpsychol 38:55-69.
2nd edition. Vol. 12-16, Mammals I-V. Gale Group, Framington Hills.
shasha, Qeen Elizabeth Park, Uganda. Zoologica Africana 7(1):233-255.
tropical cervidology: biology and medicine of Latin American deer. Jaboticabal (Brazil): Funep/IUCN.
southwestern Kenya. Mammalia 50(2): 153-164.
shire.
London.
, Giraffes, Deer and Bovids. Bloomsbury Publishing, New York.

rzewalskii) around Qinghai Lake, China. Journal of Zoology 255:175-180.

ened Species 2016: e.T136446A44142964. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T136446A4
relationship between pre- and postcopulatory sexual traits. Nature Communications DOI: 10.1038/ncom
Species 2008: e.T2461A9441445.http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T2461A9441445.en
Threatened Species 2016: e.T136472A44143172.http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T1364
Global Survey and Regional Action Plans. SSC Antelope Specialist Group. IUCN, Gland, Switzerland and C
n Journal of Ecology 55:21-29.

hesis, The University of British Columbia.
e observations and associated high-resolution grids. Int. J. Climatol. 25:693-712.

ology, 73(1):135-142.
s Hopkins University Press, Baltimore and London.
rns, Pronghorns, and Antlers. Springer, New York.
d Natural Resiurces, Gland, Switzerland.
idge University Press, Cambridge.
e in the Pyrenean chamois, Rupicapra pyrenaica. Animal Behaviour 75:361-369.
aica in Sierra Neveda Natural Park (southern Spain). Acta Theriologica 39(3):289-294.
es in the Artiodactyla: evolutionary relationships with sexual segregation. Evolutionary Ecology Research
rge ungulates in south-western Mongolia. Oryx, 33: 274-255.
havior of mountain goats. Canadian Journal of Zoolology 63: 2501-2506.
otheses. Biological Reviews of the Cambridge Philosophical Society 77(1):77-96.
oceedings of the Royal Society B 256:263-268.
nited, New Delhi.
ties of feral pigs, Sus scrofa (Artiodactyla: Suidae). Austral Ecology 24(5):538-543.
ago, IL, USA.

ence+Business Media, New York.
ge University Press, Cambridge.
ecies 2008: e.T3160A9643719.http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T3160A9643719.en

14.
distribution in northern Lao: implications for conservation. Oryx, 47(4):544-552.
. Koedoe 37(2):109-113.

rbart'sche, E., Stuttgart.
JCN, Gland, Switzerland.
agement of Philippine deer (Cervus mariannus) an Micronesian Islands. Mammalia 63:193-215.
mals. Lynx Editions, Barcelona, Spain.
Saudi Arabia (Mammalia: Bovidae). Zoology in the Middle East 59(3): 189-195.

UK.2008.RLTS.T42397A10695445.en

here reserve, Sikkim, India. Mammal Study. 37:173-181.

30834.en
0099434.en

8: 1-10.

6(1): 80-85.

2-407.

4142964.en
ms4184

72A44143172.en
ambridge

2(5):667-684.

Feeding style	=	type of the foraging strategy; grazer = predominatly feed on grasses, not-grazer =
Habitat type	=	type of habitat where te given species lives, open = open fields and plains, closed
Mating system	=	type of the mating system, monogamous = species where individuals have only c
Group size_mean	=	mean number of individuals per group
Male body size	=	size of the males in kg
Female body size	=	size of the females in kg

SSD values were calculated from sex specific body size data: log10(Male body size (kg)/Felmale body si
Avarage body size values for each species were calculated from sex specific body size data for the anal
Group size_mean and avarge body size were log transformed before PGLS analyses.

= predominantly feed on shrubs, leaves, berries, flowers and even some animal
d = closed habitats, like forest or shrublands
one mating partner per breeding saeson, polygamous = species where individuals have more than one m

ize (kg))
lyses: (Male body size (kg) + Female body size (kg))/2

ıate per breeding season

Social organization in ungulates: revisiting Jarman's hypotheses

Supplementary material 2

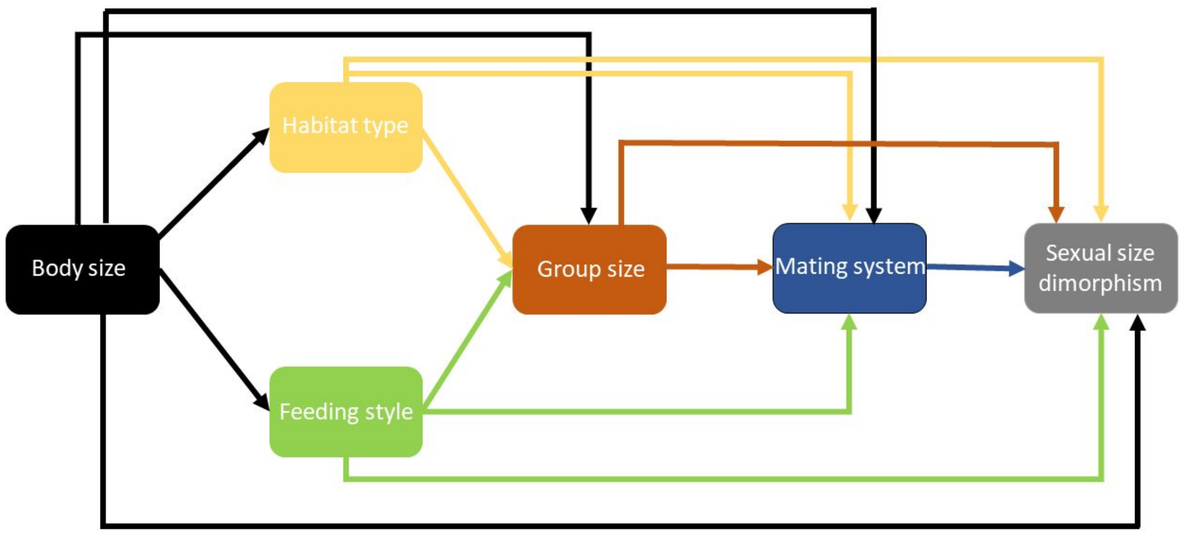
Table S1: The table represent the distribution of our variables among the Artiodactyla families. Numbers represents the number of species.

Families	No. of speci-es	Group living			Gro-up size	Habitat			Feeding style			Mating system		
		yes	*no*	*no data*		*open*	*closed*	*no data*	*grazer*	*non-grazer*	*no data*	*poly-gamy*	*mono-gamy*	*no data*
Antilocapridae	1	1	0	0	2-23	1	0	0	0	1	0	1	0	0
Bovidae	134	89	45	11	1-45	78	38	18	68	64	2	49	17	68
Camelidae	4	4	0	0	1-16	4	0	0	2	2	0	3	1	1
Cervidae	51	16	30	5	1-35	22	21	8	14	36	3	15	9	27
Giraffidae	2	1	1	0	1-50	1	1	0	0	2	0	1	1	0
Hippopotamidae	2	1	1	0	1-100	2	0	0	1	1	0	1	0	1
Moschidae	7	0	7	0	1	1	5	1	0	6	1	0	1	6
Suidae	18	14	0	4	1-300	3	9	6	0	15	3	3	0	15
Tayassuidae	3	2	0	1	2-15	0	2	1	0	3	0	0	0	3
Tragulidae	8	0	8	0	1	0	8	0	0	6	2	0	3	5

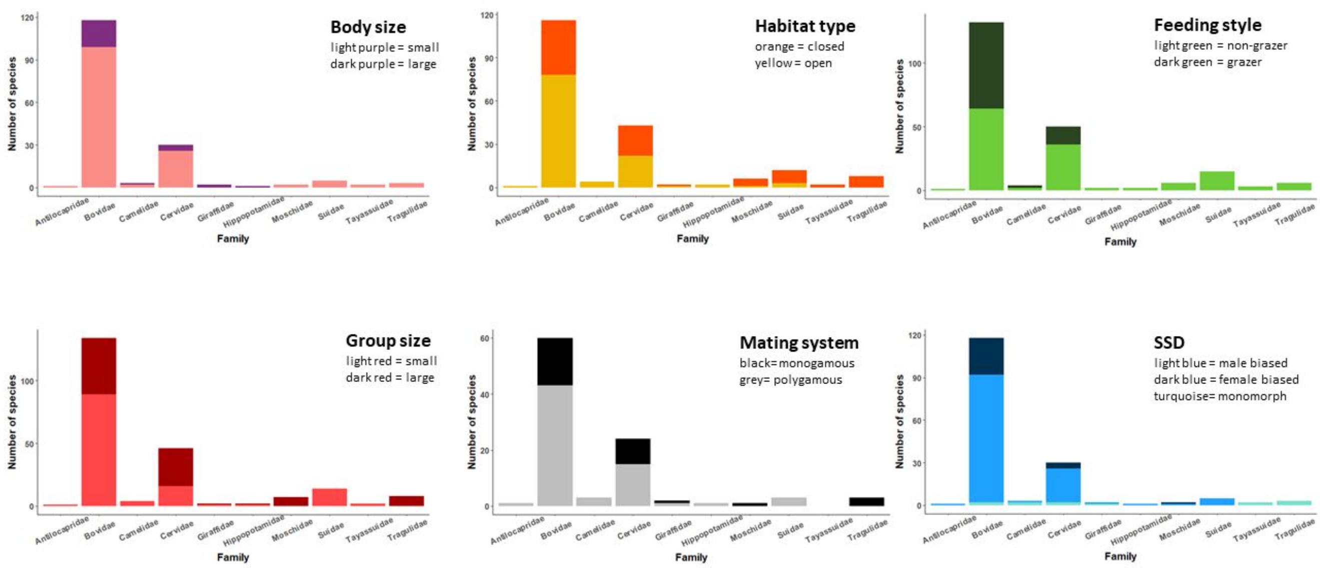
7 Table S2: Summary of path models (Fisher's C = 15.689, df= 12, p = 0.206).

Response	Predictor	Estimate	Standardized Estimate	Standard Error	df	Crit. Value	*P* value
SSD	Mating system	0.1017	0.4697	0.0187	104	5.4263	0
Mating system	Habitat type	0.3214	0.3263	0.0858	102	3.7447	0.00003
Mating system	Feeding style	-0.1588	-0.2272	0.0603	102	-2.6315	0.0098
Mating system	Group size	0.0112	0.2172	0.0046	102	2.448	0.0161
Group size	Habitat type	3.6877	0.1925	1.7862	102	2.0645	0.0415
Group size	Feeding style	-2.5788	-0.1897	1.2404	102	-2.079	0.0401
Group size	Body size	0.01	0.2467	0.0037	102	2.6665	0.0089
Habitat type	Body size	0.00005	0.2307	0.00002	104	2.4183	0.0173

Figure S1: Full initial model of the phylogenetically controlled path analysis. The model based on Jarman's (1974) hypothesis. We represent each variable and the connected pathways with different colors.



<u>Figure S2:</u> Phylogenetic distribution of ecological and social variables in ungulates. Here we collapsed the continuous variables, group size, body size and sexual size dimorphism (SSD), into binary traits as follows. In case of body size and group size we calculated the mean value of the variables: small bodied species were those which were lither than the mean value, large bodied species were heavier than the mean value. Small groups were those which have less member than the mean value, in large groups there are more individuals than the mean value. In case of SSD, if the degree of dimorphism was 0 the species was categorized as monomorphic, if the value was less than 0 we defined as female biased SSD, if the value was more than 0 we defined as male biased SSD.



<u>Figure S3:</u> Group living and its distribution among ungulate families. (A) present the number of group- living species in each family (black = solitary, grey = group living). (B) represent mean group size among the ten odd- toed ungulates family.

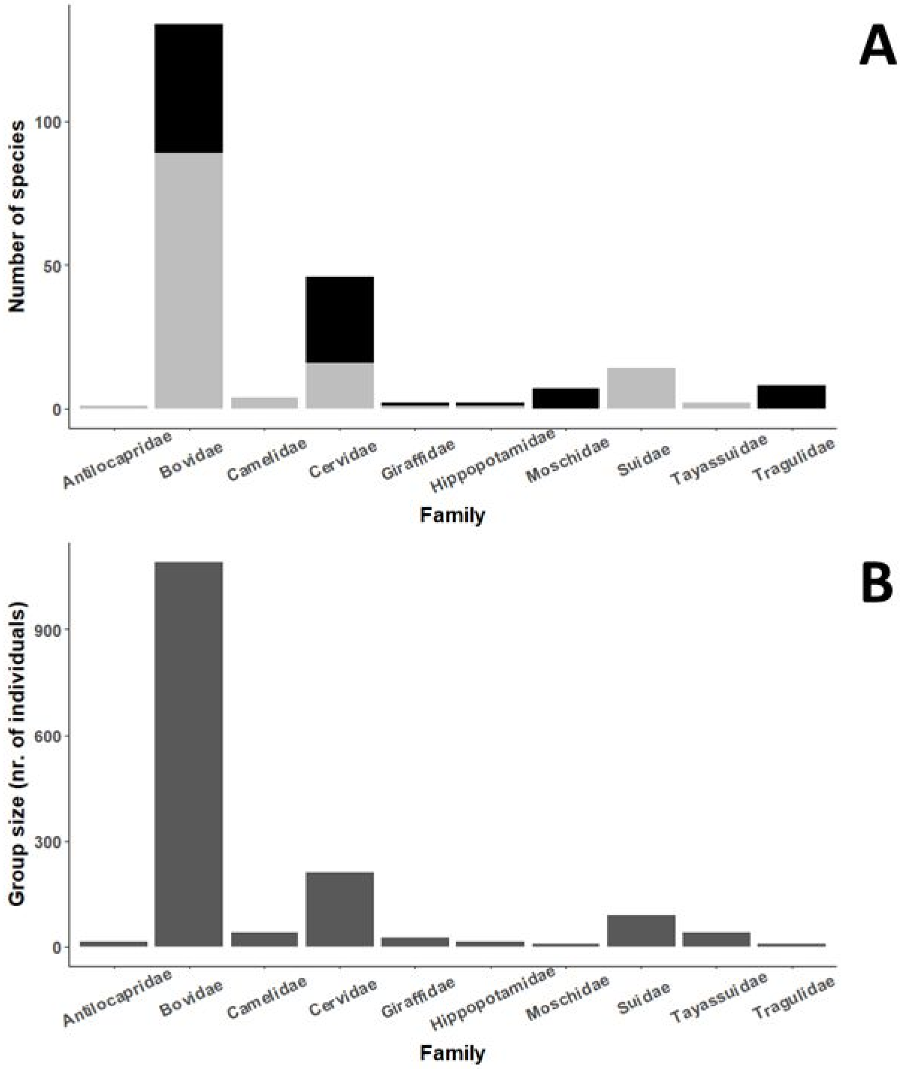


Figure S4: Species' ecology predicts (A) female (feeding style: $F = 4.42$, $df = 160$, $p = 0.037$, n = 162 species; habitat type: $F = 21.17$, $df = 148$, $p < 0.001$, n = 150 species) and (B) male (feeding style: $F = 7.31$, $df = 163$, $p < 0.001$ n = 165 species; habitat type: $F = 25.11$, $df = 151$, $p < 0.001$, n = 153 species) body mass in Artiodactyla.

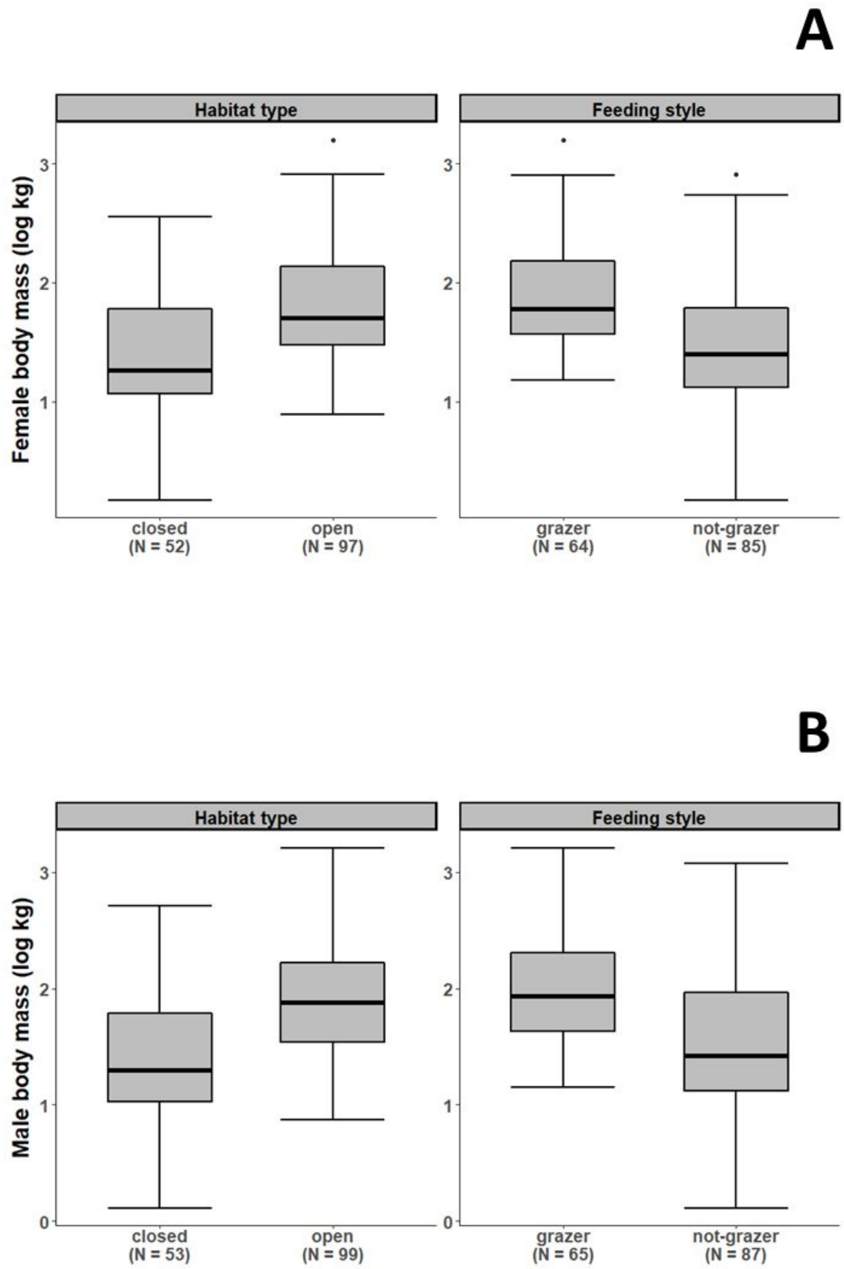
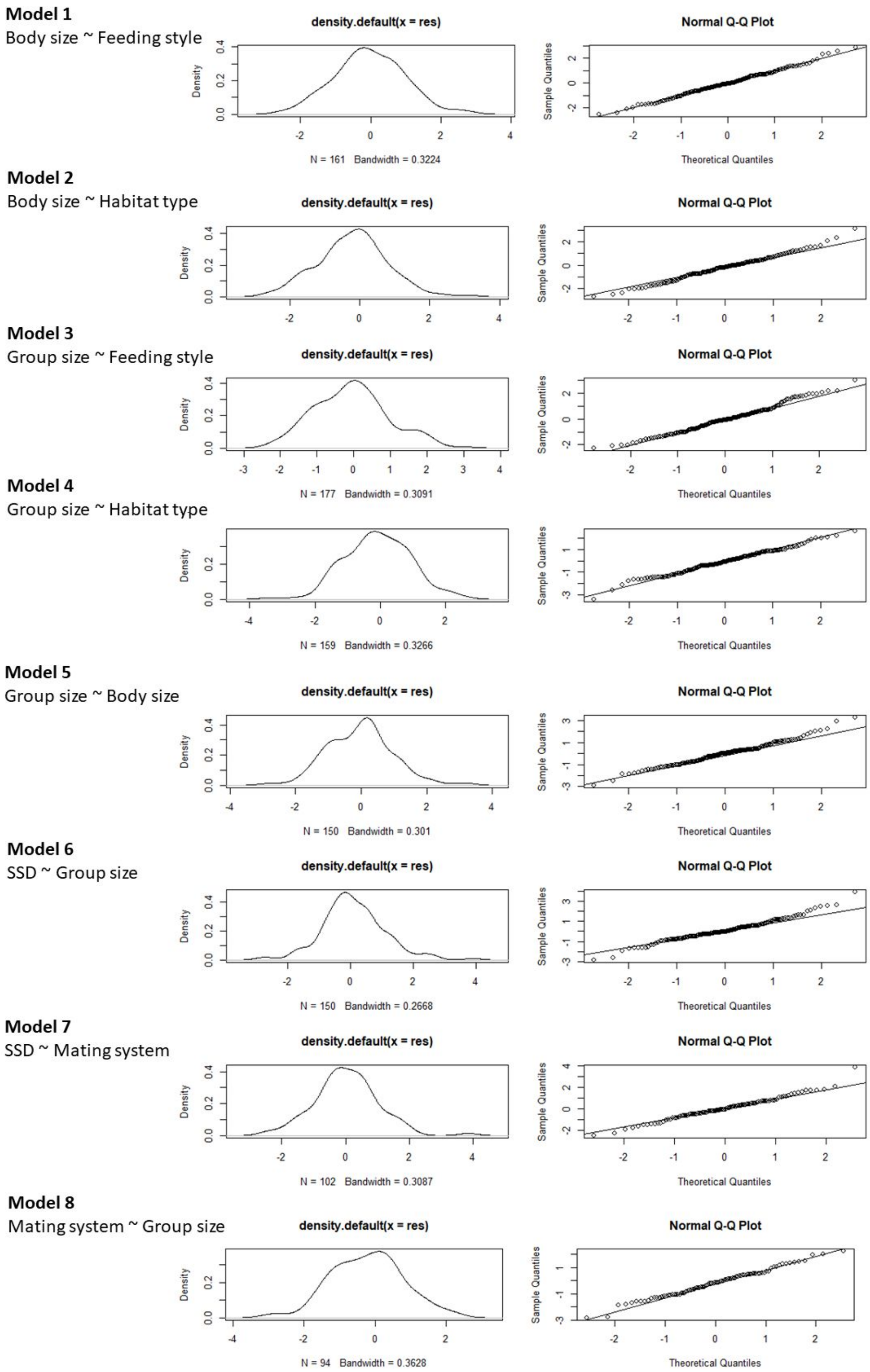


Figure S5: Distribution of the eight bivariate PGLS models' (described in Table 1) residues.



Ecology of social organisation in ungulates (antelopes, deer, bovids and relatives)